Universitat de les Illes Balears

Instituto Español de Oceanografía

DOCTORAL THESIS

2015

SETTLEMENT AND POST-SETTLEMENT PROCESSES OF MEDITERRANEAN LITTORAL FISHES: INFLUENCE OF SEASCAPE ATTRIBUTES AND ENVIRONMENTAL CONDITIONS AT DIFFERENT SPATIAL SCALES

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Doctor by the Universitat de les Illes Balears

Aquesta tesi va ser possible gràcies al conveni de col·laboració entre el Govern dels Illes Balears i l'Institut Espanyol d' Oceanografia per a la posada en marxa i el desenvolupament científic de l'Estació d'investigació Jaume Ferrer (La Mola, Menorca). El dia 1 de novembre de 2010 es va publicar al BOE núm 264 la resolució de l'Institut Espanyol d' Oceanografia de la convocatòria d'un ajuda per a la formació de personal investigador, en el marc del Pla Nacional d'Investigació Científica, Desenvolupament i Innovació Tecnològica (I + d + i), per al període 2008-2011 i del Pla de Ciència Tecnologia i Innovació (PCTI) de les Illes Balears 2009-2012. El 07 de març de 2011 es va publicar la resolució final de la concessió de l'ajuda de formació a favor de la Srta. Isabel Amalia Cuadros Casado. Aquesta tesi doctoral va ser desenvolupada entre els anys 2011 i 2015.

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Esta tesis fue posible gracias al convenio de colaboración entre el Govern de les Illes Balears y el Instituto Español de Oceanografía para la puesta en marcha y el desarrollo científico de la Estación de investigación Jaume Ferrer (La Mola, Menorca). El día 1 de noviembre de 2010 se publicó en el BOE nº 264 la resolución del Instituto Español de Oceanografía de la convocatoria de un ayuda para la formación de personal investigador, en el marco del Plan Nacional de Investigación Científica, Desarrollo e Innovación Tecnológica (I+D+i), para el periodo 2008-2011 y del Plan de Ciencia Tecnología e Innovación (PCTI) de las Illes Balears 2009-2012. El 07 de marzo de 2011 se publicó la resolución final de la concesión de la ayuda de formación a favor de Dña. Isabel Amalia Cuadros Casado. Esta tesis doctoral fue desarrollada entre los años 2011 y 2015.

To those colleagues who with their enthusiasm and effort, gave their time in pursuit of a dream, the knowledge of our Earth, and for the salvation of the world in which we live, and which sometimes were excluded and wounded in their ways by the blinded Society. It makes us all lose the opportunity to live in a more fair, solidary and beautiful world.

«Astronomy defined our home as a small planet tucked away in one corner of an average galaxy among millions; biology took away our status as paragons created in the image of God; geology gave us the immensity of time and taught us how little of it our own species has occupied». Stephen Jay Gould, Ever since Darwin (1977).

«The world is full of signals that we don't perceive. Tiny creatures live in a different world of unfamiliar forces. Many animals of our scale greatly exceed our range of perception for sensations familiar to us. […] What an imperceptive lot we are. Surrounded by so much, so fascinating and so real, that we do not see (hear, smell, touch, taste) in nature, yet so gullible and so seduced by claims for novel power that we mistake the tricks of mediocre magicians for glimpses of a psychic world beyond our ken. The paranormal may be a fantasy; it is certainly a haven for charlatans. But “parahuman” powers of perception lie all about us in birds, bees, and bacteria». Stephen Jay Gould, The Panda´s Thumb (1980).

«We pass through this world but once. Few tragedies can be more extensive than the stunting of life, few injustices deeper than the denial of an opportunity to strive or even to hope, by a limit imposed from without, but falsely identified as lying within». Stephen Jay Gould, The Mismeasure of Man (1996).

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Resum

La mar Mediterrània és un dels mars més rics del món. No obstant això, és també un dels més amenaçats. En aquest mar, les poblacions de peixos litorals, particularment d´ espàrids i làbrids, juguen un important paper econòmic i ecològic. No obstant això, la perpetuació d'aquestes poblacions pot estar limitada, entre altres causes, per l´abastiment de juvenils, ja que els seus hàbitats, en contrast amb els habitat adults, es troben a la franja costaner de menor profunditat, on les pressions antròpiques són majors. La bibliografia identifica tres hàbitats molt comuns a les nostres costes com a zones de desenvolupament dels juvenils d'aquestes espècies: les praderies marines, els boscos d'algues erectes i les zones mixtes de sorra, còdols i roques.Davant l'amenaça de la transformació antròpica d'aquests hàbitats, aprofundir en el coneixement dels factors que influeixen en la distribució de densitats de juvenils en aquests hàbitats és fonamental. Amb aquest ànim, es va dur a terme el monitoratge dels peixos juvenils durant les estacions càlides de 2011, 2012 i 2013 a l'illa de Menorca (Illes Balears). Les anàlisis exploratòries i inferencials van indicar que a una escala menor del paisatge submarí, la variabilitat en els patrons de distribució de densitats dels juvenils dins de cada hàbitat podia ser explicada per l'estructura de l'hàbitat, tant de les praderies de *Cymodocea nodosa*, com dels boscos de *Cystoseira* spp. i dels fons mixtos de sorra, còdols i roques. Les diferents espècies de làbrids i espàrids van respondre de forma contrastada a aquest factor, presumiblement a causa de que cada espècie troba el millor compromís entre disponibilitat d'aliment i refugi (qualitat de l'hàbitat) en un diferent grau d'estructuració. Així mateix, en els boscos de *Cystoseira* spp., que a Menorca s'estenen fins als 15 metres de profunditat, les dades van indicar una preferència taxa- especifica per diferents rangs de profunditat. Finalment a una escala major, la configuració de la costa, determinada en primer terme per l'exposició, va influir notablement les densitats de juvenils, probablement afectant l'arribada de larves; en segon lloc, l'orientació de la costa respecte a la direcció dels vents forts va influenciar la seva dinàmica, impedint l'arribada de larves o expulsant dels hàbitats juvenils. Conseqüentment, aquesta tesi posa de manifest la importància de considerar factors que operen a diferents escales influenciant la densitat de juvenils. En paral·lel a aquest resultat global, aquesta tesi defensa la importància de tenir en compte les diferents escales del paisatge submarí per establir plans de gestió, i aprofundir en la problemàtica de la preservació de les poblacions de juvenils en els tres hàbitats.

Abstract

The Mediterranean sea is one of the richest seas in the world. However, it is also one of the most threatened. In this sea, coastal fish populations, particularly sparids and labrids, play an important economic and ecological role. However, the perpetuation of these populations is limited, among other reasons, by juvenile settlement and recruitment. As juveniles habitats, in contrast to those of adults, are found in shallow coastal areas, they are more exposed to human impacts. Three very common habitats are identified in the literature as habitats for juveniles of these species in the Mediterranean: seagrass meadows, erect algae forests and shallow mixed areas of sand, pebbles and rocks. Faced with the anthropogenic transformations of these habitats, it is crucial a further understanding of the factors that influence the distribution of juvenile densities in these habitats. With this aim, juvenile fishes were monitored during the warm seasons of 2011, 2012 and 2013 in Minorca island (Balearic archipelago). Exploratory and inferential analyses of the data highlighted that at lower scales of the seascape, the variability of the juvenile density distribution patterns among a given habitat could be explained by variations of its structure, for *Cymodocea nodosa* meadows, *Cystoseira* spp. forests and shallow mixed bottoms of sand, pebbles and rocks. Different species of labrids and sparids responded differently to this factor, presumably because each species find the best compromise between availability of food and shelter (habitat quality) in different habitat structure conformation. Furthermore, in *Cystoseira* forests, which in Minorca extend until 15 meters depth, data highlighted some taxa-specific preferences for different depths ranges. Moreover, at larger spatial scales, the configuration of the coast, first in terms of exposure, shaped densities of juveniles, presumably affecting the initial larval input; secondly, coast orientation to strong winds influenced juveniles' dynamics, impeding larval arrival or taking out larvae from juvenile habitats. Consequently, this thesis highlights the importance of considering forcing factors at different spatial scales in order to better explain the density distribution of juveniles. In parallel to this overall result, this thesis defends the importance of taking into account the different scales of the seascape in the management planning, and delves into the issue of preserving juvenile stocks of the three studied habitats.

Resumen

El mar Mediterráneo es uno de los mares más ricos del mundo. Sin embargo, es también uno de los más amenazados. En este mar, las poblaciones de peces litorales, particularmente de espáridos y lábridos, juegan un importante papel económico y ecológico. Sin embargo, la perpetuación de dichas poblaciones está limitada, entre otras causas, por su reabastecimiento a través de los juveniles, cuyos hábitats, en contraste con los adultos, aparecen en las franjas costeras de menor profundidad, donde las presiones antrópicas se concentran. Tres hábitats muy comunes de nuestras costas son indicados en la literatura como hábitats donde los juveniles de dichas especies se desarrollan: las praderas marinas, los bosques de algas erectas y las zonas mixtas de arena, cantos y rocas. Ante la amenaza de la transformación antrópica de estos hábitats, ahondar en el conocimiento de los factores que influyen en la distribución de densidades de juveniles en éstos hábitats es fundamental. Con este ánimo, se llevo a cabo el monitoreo de los peces juveniles durante las estaciones cálidas de 2011, 2012 y 2013 en la Isla de Menorca (Islas Baleares). Los análisis exploratorios e inferenciales indicaron que a una escala menor del paisaje submarino, la variabilidad en los patrones de distribución de densidades de los juveniles dentro de cada hábitat podía ser explicada por la estructura del hábitat, tanto de las praderas de *Cymodocea nodosa*, como de los boques de *Cystoseira* spp. y de los fondos mixtos de arena, cantos y rocas. Las diferentes especies de lábridos y esparidos respondieron de forma contrastada a este factor, presumiblemente debido a que cada especie encuentra el mejor compromiso entre disponibilidad de alimento y refugio (calidad del hábitat) a distinto grado de estructuración. Asimismo, en los bosques de *Cystoseira* spp., que en Menorca se extienden hasta 15 metros de profundidad, los datos indicaron una preferencia taxa-especifica por distintos rangos de profundidad. Por último, a una escala mayor, la configuración de la costa, primeramente en términos de exposición, determinó las densidades de juveniles, probablemente afectando la llegada de larvas; en segundo lugar, la orientación de la costa respecto a la dirección de los vientos influenció su dinámica impidiendo la llegada de larvas o expulsándolas de los hábitats juveniles. Consecuentemente, esta tesis pone de manifiesto la importancia de considerar factores que operan a distintas escalas influenciando la densidad de juveniles. En paralelismo a este resultado global, esta tesis defiende la importancia de tener en cuenta las diferentes escalas del paisaje submarino para establecer planes de gestión, y ahonda en la problemática de la preservación de las poblaciones de juveniles en los tres hábitats estudiados.

Chapter I. General Introduction

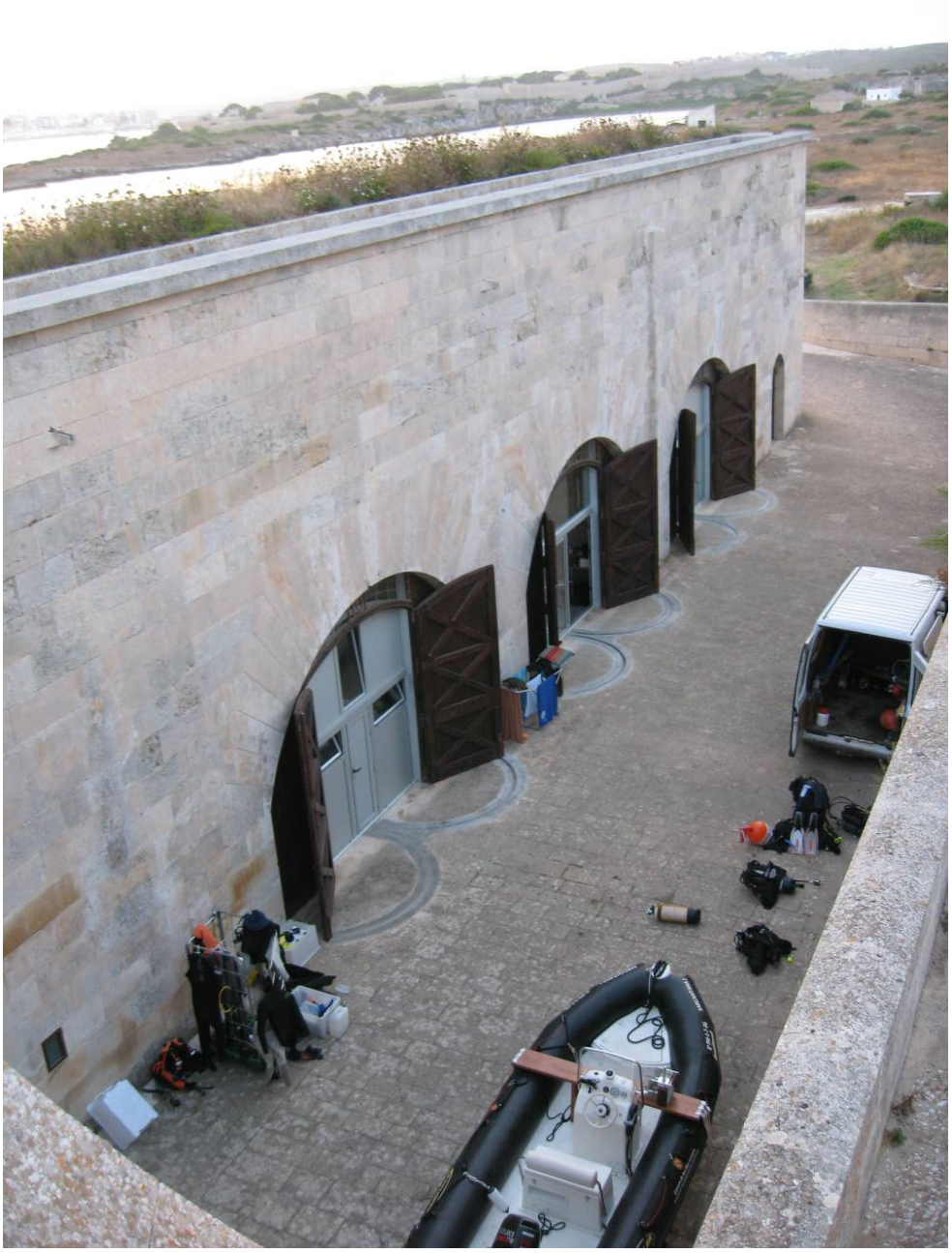

Photo I-1. Estació d´Investigació Jaume Ferrer, Marine Station of the Centre Oceanogràfic de Balears (COB), Instituto Español de Oceanografía (IEO). July 2011. Photo: Adrien Cheminée.

Chapter I. General introduction

I.1. CONTEXT OF THE STUDY

I.1.1. Natural processes and the importance of spatial and temporal scales

The main objective of natural sciences is to find patterns, i.e., particular configurations of the characteristics of a given system, or from a statistical point of view, the particular configuration of the response variable(s). Subsequently natural sciences aim to understand the causes of such patterns, i.e., the systematic series of actions which leads to this particular configuration, called processes (Wiens, 1992). And, finally, natural sciences try to detect possible factors (independent variables) which influence such processes and patterns.

However, the patterns that we observe in nature and the processes or factors that cause or modify respectively those patterns change according to the spatial and/or temporal scale of our observations and experiments. For example, within a given region, temperature (i.e. the response variable) vary between vegetated areas, with less extreme temperatures, and denudated areas, with more extreme temperatures (i.e. the factor), due to the regulation produced by the canopy shadowing and evapotranspiration (i.e. the process) (Myers, 1997). At larger spatial scales, temperature increase from the Poles to the Equator due to the different irradiation angle (factor) (Kottek et al., 2006). At the scale of the planet, the albedo surface or reflection surface (factor) influences global temperatures, increasing the greenhouse effect (process) (Foley et al., 2005; Gash and Shuttleworth, 1991). As regards to temporal scales, the mean atmospheric temperature increases quickly since the 1800s due to the increase of the strength of the greenhouse effect (process), because of the increase of the CO_2 emissions and the increase of albedo surfaces due to the Industrial Revolution (factors). But when we observe the records of temperatures thought the history of planet Earth, cyclical changes in temperature happen because of the inter-glaciations and glaciations events every 100.000 years governed by cyclic orbital variations (process) (Farley, 2008). In the same way, plant transpiration also changes according to temporal and spatial scales. The variation of transpiration rates are a consequence of physiological

mechanisms (process). At the scale of a given leaf surface, transpiration rates are influenced by the stomatal distribution (factor). Whereas variations of transpiration rates among different regions of the world are consequence of climate (factor). As a regards to temporal scales, transpiration rates during one day are regulated by light and temperatures (factors). Seasonally, transpiration rates are regulated additionally by the seasonal variations of the leafs, since their birth until their senescence (factor) (Moro et al., 2004).

Consequently, since patterns change with the spatio-temporal scale of our observation, there is not a single natural scale at which a given phenomena should be studied. However, it is not possible to encompass all spatio-temporal scale levels to study a given phenomena, and even more, patterns frequently do not change in every level of a given spatio-temporal scale. Indeed, in some cases the patterns must be understood as emerging from the collective behaviors of the assemblage of smaller scale processes (e.g. the building of mountains). To limit our spatio-temporal scales of study in order to describe and understand natural patterns, study processes and influencing factors, it is firstly important to take into account the nature of the investigated phenomena *per se* (see examples in Fig. I-1) (Wu, 1999).

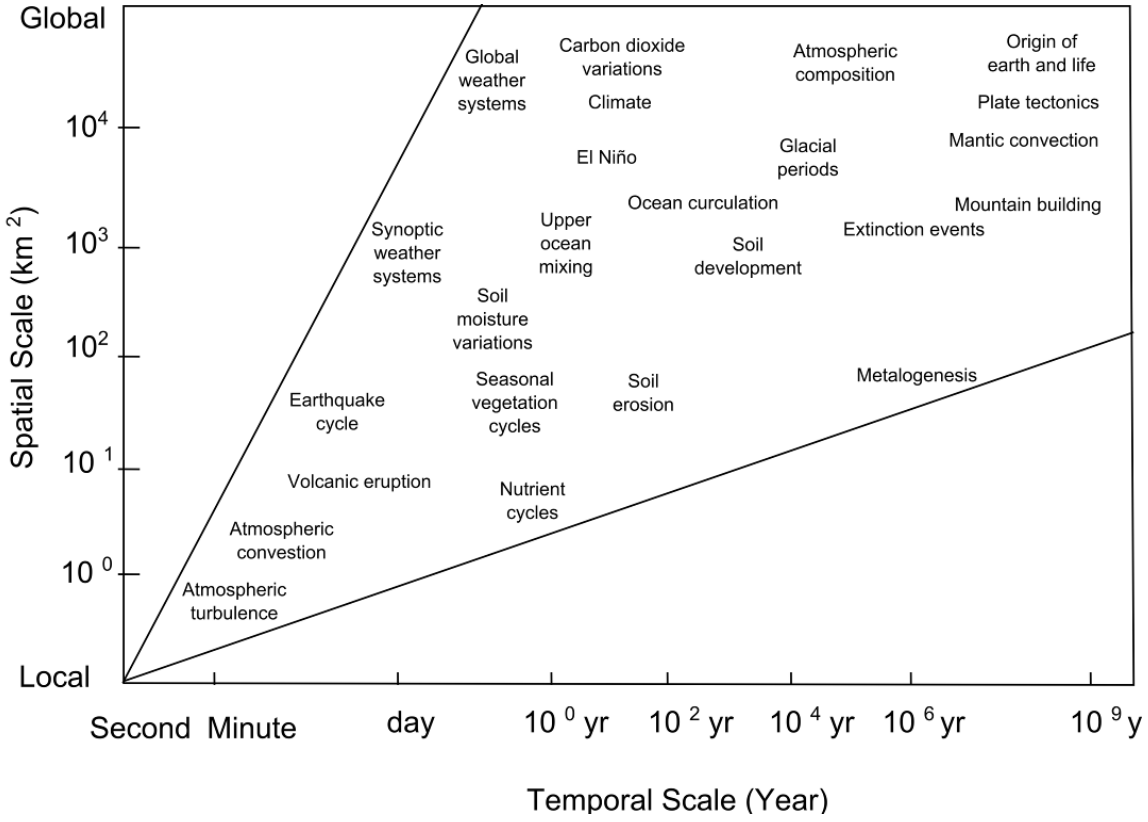

Fig. I-1. Spatio-temporal scale at which different physical and ecological phenomena occur.Physical and ecological phenomena tend to line up, approximately, along the diagonal direction in the space-time scale diagram although variations may sometimes be large – modified from (Wu, 1999).

I.1.2. The case of species density distribution patterns

The importance of habitat, biological interactions and physical factors in the framework of life-cycles

In the case of the density distribution patterns of any given species, their variability is the result of processes that operate at different spatial and temporal scales: dispersal, birth and survival rates (Collins and Glenn, 1991; Guo et al., 2005; Kareiva et al., 1990), but in the framework of multi-generational time scale and spatial scales large enough to encompass all stages of the life-cycle of such species (Cooper et al., 1998; Di Franco et al., 2013). Consequently, to delimitate the temporal scale in studying dynamics for a given species, the duration of its life-cycle must be taken into account. To delimitate the spatial scale in studying dynamics for a given species, the seascape or landscape "perception" of the species and more particularly the habitats were species occur in the seascape or landscape must be considered (Bostrom et al., 2011).

Habitats are defined as the assembly of the biotope and biocenosis, which shapes a particular configuration (Chapman, 1995). In this definition, habitat concept is not organism-specific (but see other definitions, e.g. Hall et al. (1997), which defined habitat as "the resources and conditions present in an area that produce occupancy-including survival and reproduction-by a given organism"). Landscape or seascape is the assembly of a mosaic of habitats (terrestrial or marine respectively). In this mosaic, a "suitable habitat" for a given species, is an habitat within which the species can potentially or does occur (Delong and Gibson, 2012). The entire life-cycle of a species may take place in a given suitable habitat, or alternatively in various suitable habitats. For example, elephants spend the various stages of their life cycle in the same collection of habitats (Stokke and Toit, 2002); whereas amphibians change of habitat throughout their life cycle (Vonesh and De la Cruz, 2002).

Furthermore, among seascapes or landscapes, each habitat, and more particularly, each suitable habitat for a given species is characterized by its three-dimensional structure: that is the physical arrangement of objects in the space (Bell et al., 1991). This habitat structure is composed by complexity (absolute abundance of individual structural components) and heterogeneity (relative abundance of different structural components) under a determinate spatio-temporal scale (Beck, 2000; Bell et al., 1991; Byrne, 2007).

And at lower scale, within a given habitat, habitat display patchy variations of its three-dimensional structure. The scales at which species density patterns respond to habitat structure depend on the scale at which organisms or life-cycle stages "perceive" the changes of habitat structure (e.g. an arachnid *versus* a rabbit, which inhabits in the same scrub; a butterfly larvae *versus* an adult butterfly which inhabits the same grassland); this in turn is related with the scale at which habitat provide conditions appropriate for individual and population persistence (Hall et al., 1997); such conditions, i.e. mainly food and shelter availability, define the habitat quality (Hindell et al., 2000). For many species more structured habitat are high quality habitats since they provide better refuges against predation and more food which facilitates rapid growth and consequently reduce predation risk according to the stage-duration hypothesis (Hyslop et al., 2012; Vigliola, 1998). For example, the endangered Bridled nailtail wallabies *Onychogalea fraenata* density distribution patterns reflect a preference for wooded edges *versus* open habitats since such habitat provide a good trade-off between shelter and food for such species (Fisher, 2000); for the same reasons the Mediterranean lizard *Psammodromus algirus* density distribution patterns reflects a preference for higher sized shrubs (Diaz and Carrascal, 1991). There are many examples which support the effects of habitat structure in determining density patterns of species (August, 1983; Dennis et al., 1998; Sanders et al., 2008; Stamps, 1983).

Suitable habitats and habitat quality strongly influence density distribution patterns, since they influence dispersal, survival and reproduction success of a given organism (Bowler and Benton, 2005; Hall et al., 1997). Furthermore dispersal, survival and reproduction processes are influenced by biological interactions (competency, predation, parasitism, etc.), which may affect at local and/or broad scales (Wiens, 1989). For instance, the density distribution patterns of the bird Least Flycatchers (*Empidonax minimus*) and the American Redstart (*Setophaga ruticilla*) have a locally segregated distribution due to inter-specific competitiveness; however, at larger scales, habitat selection override the local effects of biological interactions, and both species occurs in the same regions (see such and other examples in Wiens (1989)).

Finally, the environmental physical factors influence density distributions. Even for a given species, some responses will be to a narrow range of environmental influences, and others will be diffusely linked to a broad range of influences (Levin, 1992). Environmental physical factors may also act at local and/or broad scales: for instance, Wiens (1989) explained that "the relationships between climate and vegetation may disappear at finer

scales overridden by the effects of competition and other biological processes" (see reference and their examples therein).

Let's consider some examples of how suitable habitat is perceived at different scale according to organisms and life cycle stage, and how biological interactions and physical factors influence the density patterns distribution of different organisms at different temporal moments in the framework of their life cycles.

The loggerhead sea turtle, *Caretta caretta*, is widely distributed in subtropical regions (Pritchard et al., 1997); among birds, the barn swallow (*Hirundo rustica*) is distributed in both north and south hemispheres and the mammalian Iberian lynx (*Lynx pardinus*) is restricted to the south of Iberian Peninsula (UICN, 2015). The loggerhead sea turtle develops its life cycle in seascapes; whereas the other two species develop their life-cycle in continental landscapes. The suitable habitat for these three species is different and changes throughout their life-cycle. The first one, *Caretta caretta*, occupies three different habitats during its life: beaches, neritic zone with seagrass meadows (nearshore coastal areas) and oceanic zones far from coastal areas. Life cycle starts when a female lays its eggs on a nesting beach (Heppell, 1998). Juvenile turtles move to neritic habitats before reaching sexual maturity, and adults migrate periodically between neritic foraging sites and nesting rookeries (Bolten, 2003). The life-cycle of one turtle until its first reproduction spends at least ~17-30 years. The barn swallow occupies two different habitats: the breeding habitats and the winter habitats. They breed across the northern hemisphere in warmer sessions, foraging mainly on farmland and nesting in old buildings, particularly those associated with livestock (Møller, 2001). During the northern hemisphere winter, they migrate to open fields of the southern hemisphere (UICN, 2015). The life-cycle of one barn swallow until its first reproduction spends at least ~1 year. The Iberian lynx mainly inhabits in Mediterranean scrubland habitat, however it may use other habitats throughout its life-cycle. Juveniles and adults without territory accomplish dispersal phases until they become stable in some areas (Palomares et al., 2000). During dispersal and after dispersal they occupy also Pine forests habitats. The life-cycle of one Iberian Lynx until its first reproduction spends at least ~2-3 years. As a conclusion, different species have different suitable habitats and display different life-cycle durations, consequently, a different spatio-temporal scale is needed to study their dynamics and density distribution patterns.

The influence of biological interactions on density distributions changes according to species and its life cycle stage. For example, predation processes are very important influencing densities of Loggerhead sea turtle, but mainly during its early phases (Dodd, 1988). Intra-specific competition interactions are important influencing density-distributions of Lynx, mainly in its dispersal phases (both juveniles and adults) (Gaona et al., 1998). Parasitism and infanticide are mainly important influencing densities of the barn swallow in the breeding phases (parasitism affects nests of such species) (Møller, 1987).

The influence of environmental physical factors on density distributions also changes according to species and their life cycle stages. For the Loggerhead sea turtle, currents have an important effect, mainly for immature individuals, which have limited swimming skills, and therefore, density distribution of immature individuals reflects mainly water masses circulation patterns (Carreras et al., 2006; Revelles et al., 2007). For barn swallow, adverse weather causes high depletion of its populations. It occurs due to storm episodes en route and cold weather after arrival or before departure from breeding areas (Moller, 1989; Newton, 2007). For the Iberian Lynx the loss and fragmentation of its habitats are probably the most important forcing factor determining its density distributions, since it interferes during dispersal phases of such species (Ferreras, 2001).

The salient point of these examples is that each organism considers a different habitat as suitable habitats, depending on its life stage, and the influence of biological interactions and physical environment in determining population dynamics varies specifically, spatially and temporally. To take into account the entire life cycle of species is determinant to understand the role of habitats and the processes or factors which control (and may limit) the replenishment of populations.

In this sense, the carrying capacity of an habitat for a given species is considered as the maximum population size of the species that the habitat can sustain indefinitely, given the resources available in the habitat which fits with the necessities of each species (Hickman Jr. et al., 2013). However, the carrying capacity of a given habitat for a given species, as illustrated by the previous examples, may as well be shaped by processes occurring in the previous habitats. In this sense, for species which use separate habitats at juvenile and adult stages, juvenile habitats could be a bottleneck for the replenishment of adult populations (Halpern et al., 2005). For example, the snow geese (*Chen caerulescens*) dynamic is highly influenced by breeding habitats, which occur in arctic wetlands habitats. Populations were

self-regulated in traditional breeding areas, where the increase of population leaded to a degradation of its juvenile habitats, therefore causing a periodical declines on the production of juveniles (Cooch et al., 1993; Williams et al., 1993). However, the development of agriculture, which extends rice-culture fields, has caused a rupture in this equilibrium, providing greater availability of habitat for breeding and juveniles. As a consequence, population has grown dramatically (Cooch et al., 1993), and has been reported to cause an important destruction of its winter quarters in southern areas and in its traditional breeding areas (Gauthier et al., 2005; Kerbes et al., 1990; Peterson, 2013).

I.1.3. The case of marine fishes and their juveniles

As respect to our case of study, marine teleost fish species display various life strategies: they may be oviparous, viviparous, with internal or external fecundation. However, most of marine fish are oviparous with external fecundation (Hickman Jr. et al., 2013). Females spawn eggs into the water column or on the substratum, which are then fertilized by males. Eggs and subsequent larva, for many species, stay in the water column, and are dispersed by currents (Hannan and Williams, 1998; Jenkins et al., 1997). Some species stay in the pelagic environment for their entire life (Hickman Jr. et al., 2013). However, others present a bipartite life cycle consisting of such pelagic phase in which eggs and larvae are dispersed by currents and a subsequent and more site-attached phase in which juveniles develop into adults (Thresher et al., 1989; Vigliola et al., 1998). Such organisms are benthic species. For these organisms, the post-larval period is delimited by two landmark events: settlement and recruitment. Settlement is a biological period at which pelagic larvae become associated with benthic substrates. It occurs after larvae metamorphosis, marking the end of the pelagic larval phase. “Settlers” refers to these recently settled individuals or early juveniles. Upon survival and growth these early juveniles develops into late-juveniles that are, therefore, older juveniles already adapted to a benthic life and ready to join adult populations in a process called “recruitment” (Connell, 1985; Levin, 1994; Macpherson, 1998; Thiriet, 2014).

Furthermore, although there are some exceptions (Guidetti and D´Ambrosio, 2004), many marine fish, including both pelagic and benthic fish, present different habitats at adult and juvenile phases. For example, the Pacific sardine (*Surdinops sugux cueruleus*) in the Gulf of California present a cycle where juveniles concentrate in the Baja California coast, and

later on, when their development is accomplished, they migrate to the northern adult feeding grounds (Hammann et al., 1988). In other cases, tropical coral reef fish species present a cycle where juveniles develop among shallow seagrass beds and mangrove habitats, and hereafter migrate to deeper coral reef systems (Gillanders et al., 2003; Huijbers et al., 2013; Nagelkerken, 2009; Nagelkerken et al., 2000). In Mediterranean ecosystems, many juvenile fish also occupy a narrower depth ranges than adults and appear associated with specific coastal habitats (García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Verlaque, 1990).

Among habitats where juveniles of a given species may dwell, those habitat that have a "nursery role" are those which provide on average per unit area, the greatest amount of new individuals that effectively integrate adult populations, i.e. those which display a higher "nursery value" *sensu* Beck et al. (2001). For a given habitat, for a given species, in a given site, its nursery value is the result of various components including the initial juvenile density (i.e. settlers in benthic fish) and their subsequent survival, growth, and dispersion capacity (connectivity) (Beck et al., 2001; Heck et al., 2003). However, habitats that may have a small per-unit-area contribution to adult populations may be critical as well for sustaining adult populations, for example, because of their wide area. In this sense, Dahlgren et al. (2006) propose the term "Effective Juvenile Habitat" (EJH) to describe juvenile habitats that in terms of their overall contribution, are important for maintaining adult populations. Moreover, other authors supported that it is the contribution to the production of succeeding generations that determines real "nursery-ground value" (its fecundity), instead to just the numbers of adults individuals provided by a given habitat (Layman et al., 2006; Sheaves et al., 2006). Furthermore, Nagelkerken et al. (2015) argued that the nursery role or the EJH approaches fail to incorporate dynamic processes, such as ontogenetic habitat shifts, juvenile movement and spatially explicit usage of habitat patches and corridors, since these concepts are centred in the habitat as unit of study. Nagelkerken and his colleagues therefore introduced the term "seascape nurseries", to incorporate such processes, and it is defined as a spatially explicit seascape consisting of multiple mosaics of habitat patches that are functionally connected.

In spite of this lack of conceptual consensus, identifying juvenile habitats (i.e. habitats were juveniles potentially occur) is essential, since availability of juvenile habitats is a key issue determining adult population renewal. Indeed, availability of juvenile habitats at distances accessible to migrate to adult habitats has been reported to increase adult

populations (Huijbers et al., 2013; Nagelkerken et al., 2012). Besides, it must be understood the factors affecting the nursery value of a given habitat, i.e. shaping its spatial variability between sites; this includes understanding factors shaping initial density of settlers, their growth and survival, and latter dispersion (Beck et al., 2001). This is necessary to better understand if habitat transformations e.g. through human activities, may affect habitat nursery functions. More particularly, survival and growth within juvenile habitat are shaped by its biotic and abiotic characteristics, notably its three-dimensional structure. Indeed, as commented previously, habitat structure shapes food and refuges availability (Dahlgren and Eggleston, 2000), and then the "habitat quality". Dramatic transformations (through human impacts) of habitat characteristics and thus of habitat structure may consequently lead to lower habitat quality and thus reduce the habitat capacity to sustain juvenile production.

The case of Mediterranean labrids and sparids and their juvenile habitats

Juvenile fish Mediterranean habitats

Among the Mediterranean infra-littoral (i.e. subtidal) seascape mosaic (Musard et al., 2014), several habitats are often reported in the bibliography as fish juvenile habitats: seagrass meadows on soft bottoms, erect macroalgae forest covering rocky reefs and shallow heterogeneous mixed bottoms composed by sand, gravels, pebbles and rocks (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995) (Photo I-2). These habitats are characterized by contrasted tri-dimensional structure, notably because they are macrophyte-formed habitat or because they display heterogeneous and complex abiotic substratum.

Seagrass meadows in the Mediterranean Sea are formed by various species of seagrass: *Posidonia oceanica, Cymodocea nodosa, Zostera noltii, Z. marina, Ruppia maritima, R. cirrhosa* and *Halophila stipulacea.* The most abundant seagrasses in the Mediterranean Sea are *P. oceanica*, *Zostera* spp. and *C. nodosa*. *P. oceanica* is the most common seagrass in the open sea, forming wide and quite continuous meadows along the coasts (Telesca et al., 2015) whereas *Zostera* spp. and *C. nodosa* are more typical of shallow and sheltered to semi-exposed, marine or euryhaline, water masses. *P. oceanica* beds and, to a lesser extent, *C. nodosa* ones, are the most dominant in this region, since *Z. marina* is mostly found as

small isolated stands and *Z. noltii* mainly forms dense but sparse beds in the muddy sand of intertidal areas (Borum et al., 2004; Guiry and Guiry, 2015; Short et al., 2007).

Among the Mediterranean biocenosis of the photophilic macrophytes of the infralittoral rocky reefs, erect macroalgae forests are formed more particularly by Fucales, notably of the genus *Cystoseira*. The Mediterranean basin is considered as a hot-spot of diversity for *Cystoseira* species, where they are especially abundant and diversified (Gianni et al., 2013). They may dominate algal assemblages in the infralittoral and upper circalittoral rocky bottoms in un-impacted areas (Garreta and Martí, 2000; Giaccone, 1973; Sales, 2010). In this sense, they are one of the possible Multiple Stable States (MSS) of the rocky bottoms (Bonaviri et al., 2011). *C. brachycarpa* var. *Balearica* and *C. crinita* form extended forests in the Mediterranean (Robvieux, 2013). Erected arborescent macro-algae or seagrass species display various structural parameters and biomass (Borum et al., 2004; Guidetti et al., 2002; Robvieux, 2013) and are considered biogenic habitat former (emergent three-dimensional organisms).

Finally, the shallow heterogeneous mixed bottoms composed by sand, gravels, pebbles, boulders and rocks are distributed along all the coastlines of Mediterranean Sea, and their location is determined notably by the geomorphology of coast, i.e. usually in enclosed or semi-enclosed rocky coast-line, where the combination of terrestrial and subtidal erosion and water circulation leads to the deposition of products of mixed sizes (from sand to boulders).

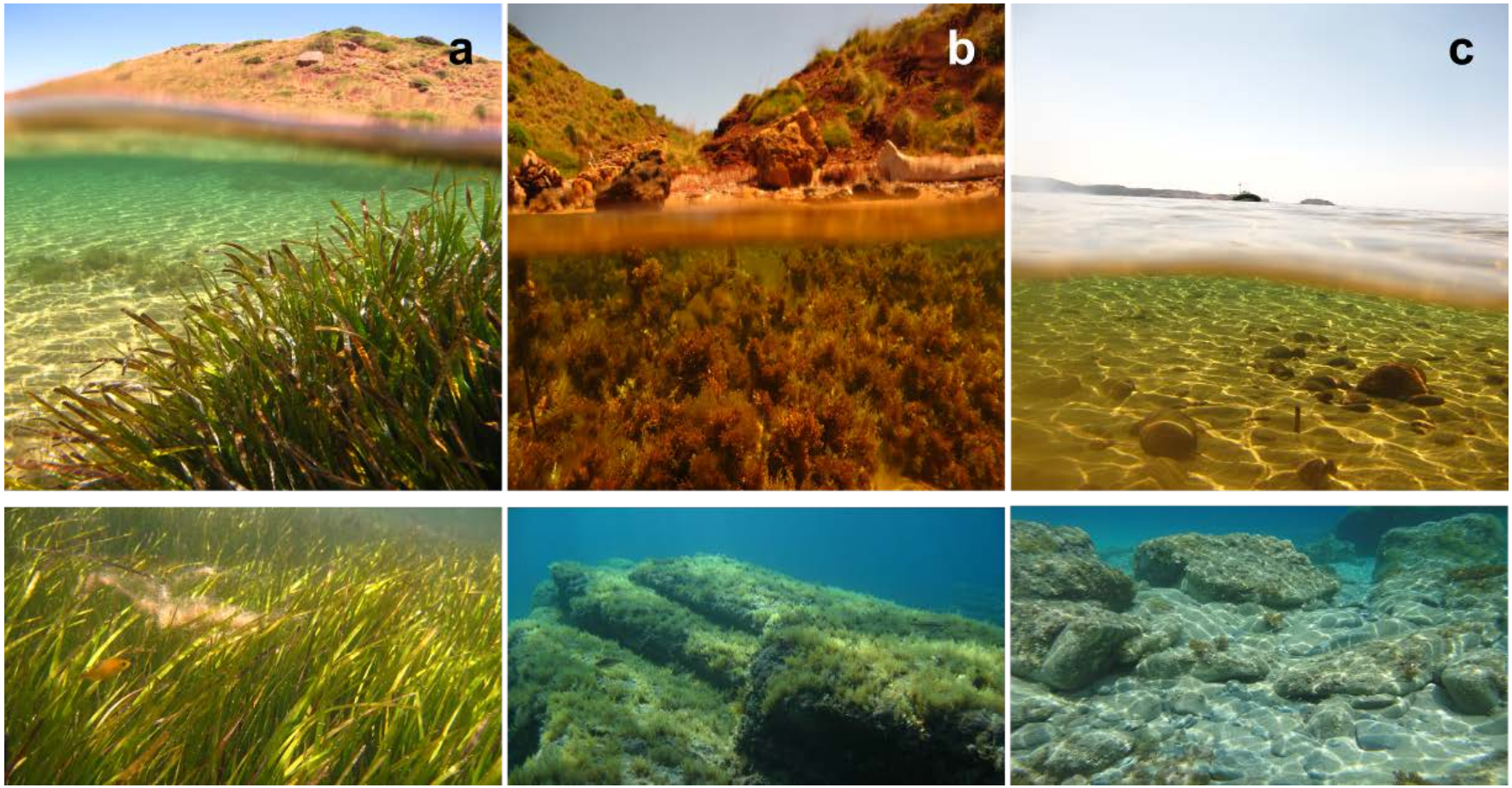

Photo I-2. Three common habitats in the patchy seascape of the infra-littoral Mediterranean Sea reported in the bibliography as juvenile habitats: seagrass meadows, erect macroalgae forests and shallow mixed bottoms composed by sand, gravels, pebbles, boulders and rocks. a) seagrass meadows (top: *Posidonia oceanica*; bottom: *Cymodocea nodosa*), b) rocky reef with *Cystoseira* spp. erect macroalgae forests and c) shallow heterogeneous mixed bottoms composed by sand, gravels, pebbles, boulders and rocks. Minorca island. Summers 2012-2013. Depth: 1-5 meters. Foreground spans around 0.5-3 m wide in each picture. Photos: Adrien Cheminée y Amalia Cuadros.

Mediterranean labrids and sparids

Many juveniles of different fish families have been reported to occur in such Mediterranean habitats: Atherinidae, Blenniidae, Gobiidae, Labridae, Mullidae, Moronidae, Pomacentridae, Serranidae, Scorpaenidae, Sparidae, Tripterygiidae (etc.) (Biagi et al., 1998; Bussotti and Guidetti, 2010; Crec´hriou et al., 2015; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). Much of these fish settle during summer (Fig. I-2), although the exact timing depends of each species (Table I-1).

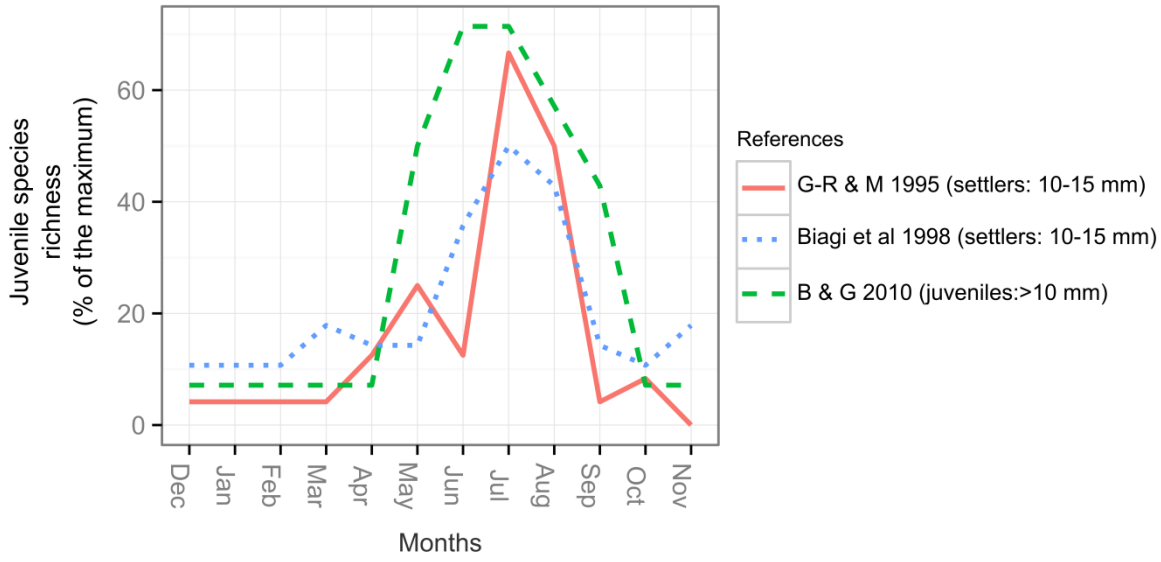

Fig. I-2. Seasonal richness of NW Mediterranean fish settlers according to various references. Percentage of the total species recorded in each paper which settles each month. References: G-R & M 1995 (García-Rubies and Macpherson, 1995); B & G 2010 (Bussotti and Guidetti, 2010) and Biagi et al. 1998. All juveniles (15 mm TL to 1/10 of TL of each species) were included for B & G 2010 because the detailed settler's presence data were not indicated in that paper.

Table I-1. Settlement seasonality in the NW Mediterranean for different fish species as recorded in the bibliography (Biagi et al., 1998; Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995). All juveniles (15 mm TL to 1/10 of TL of each species) were included for B & G 2010 because settler's presence data were not indicated in that paper. x= García-Rubies and Macpherson, 1995; shaded area= Biagi et al, 1998; framed area= Bussotti and Guidetti, 2010.

Family	Species	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Atherinidae	*Atherina* spp.												
Blenniidae	*Aidablennius sphinx*												
	Lipophrys pavo												
	Parablennius rouxi												
	Parablennius sanguinolenthus												
Gobiidae	*Aphia minuta*												
	Goboius bucchichii												
	Goboius cobitis												
Labridae	*Coris julis*								x	x			
	Ctenolabrus rupestris								x	x			
	Labrus bimaculatus					x	x						
	Labrus merula					x	x						
	Labrus viridis					x	x						
	Symphodus cinereus								x	x			
	Symphodus doderleini								x	x			
	Symphodus mediterraneus								x	x			
	Symphodus melanocercus								x				
	Symphodus ocellatus								x	x			
	Symphodus roissali							x	x				
	Symphodus rostratus								x	x			
	Symphodus tinca								x				
	Thalassoma pavo								x				
Moronidae	*Dicentrarchus labrax*												
Mullidae	*Mullus surmuletus*								x	x			
Pomacentridae	*Chromis chromis*								x	x	x		
Serranidae	*Serranus cabrilla*						x	x					
Sparidae	*Boops boops*												
	Diplodus annularis												
	Diplodus cervinus								x				
	Diplodus puntazzo											x	
	Diplodus sargus						x	x					
	Diplodus vulgaris	x	x	x	x								
	Lithognatus mormyrus								x	x			
	Oblada melanura								x	x			
	Pagellus bogaraveo												
	Sarpa salpa						x					x	
	Spondyliosoma cantharus												
Tripterygiidae	*Tripterygion* spp.												

Among these fishes, labrids (Labridae, wrasses) and sparids (Sparidae, sea breams) are two dominant groups of benthic species in the Mediterranean region (Biagi et al., 1998; Psomadakis et al., 2012). Both labrids and sparids have interest from a conservational point of view. Many species are directly subject to commercial exploitation and fisheries, or are of recreational and spear-fishing interest (Goñi et al., 2008; Lloret et al., 2008; Morales-Nin et al., 2005). Furthermore, they have important ecological roles in Mediterranean ecosystems: they are included among the important preys of many marine top-predator fishes (Reñones et al., 2002) and top-predator seabirds (Velando and Freire, 1999), and some of these species (e.g. *Diplodus* spp.) exert a top-down control on invertebrate grazers, which allow avoiding the destruction of important Mediterranean marine habitats through over-grazing (Hereu, 2004).

Previous works described that juveniles of these species display a spatio-temporal partitioning of the use of the previously mentioned habitats; species which share a given habitat at the same depth for settlement present a seasonal segregation in their settlement and *vice versa* (Biagi et al., 1998; Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995).

Globally, sparids species settle at different times through the year, primarily in the shallowest zone (0 to 2 m), preferring different bottom-types according to species: *Diplodus puntazzo, D. vulgaris*, *D. cervinus* and *D. sargus* settle among sheltered shallow and gently sloping bottoms composed by sand, gravels, pebbles or boulders, respectively in autumn, winter and spring (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995) (Photo I-3). Contrastingly, *D. annularis* and *Spondyliosoma cantharus* juveniles are mostly associated to seagrass meadows (Photo I-3); *D. annularis* settles in summer, and *S. cantharus* starts its settlement in spring. They are specially associated with small-sized seagrasses (genus *Cymodocea* or *Zostera*) (Bussotti and Guidetti, 2010). However, such species has been also observed in high densities in *P. oceanica* beds in Italy and other areas (Bussotti and Guidetti, 2010; Francour and Le Direac'h, 1994; García-Rubies and Macpherson, 1995; Guidetti et al., 1997; Guidetti, 2000). *Sarpa salpa* settles in spring and autumn as well in both mixed bottoms of sand, gravel and small blocks and seagrass meadows, but also in shallow rocky habitats (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Verlaque, 1990) (Photo I-3). Other sparid species appears as well associated with rocky substratum, for example *Oblada melanura* has been recorded to settle in summer and

presents a preference for rocky overhangs and cliffs (García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995), which may be covered by arborescent macroalgae (Bussotti and Guidetti, 2010).

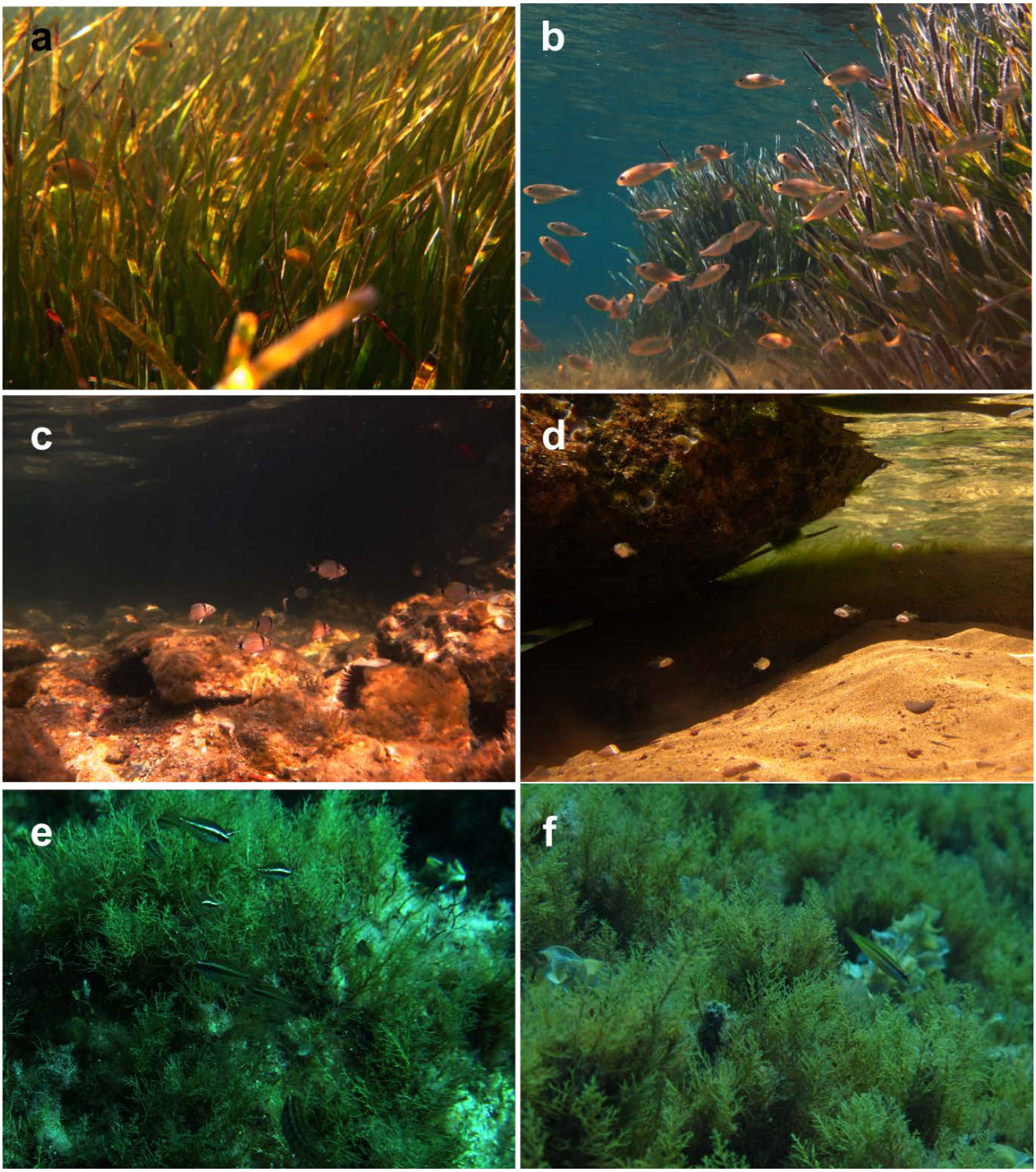

Photo I-3. Some examples of sparids and labrids juveniles among four common juvenile habitats of the infra-littoral Mediterranean Sea. a) A group of *Diplodus annularis* (25 mm TL) and one *Spondyliosoma cantharus* (50 mm TL) in a *Cymodocea nodosa* seagrass meadow (July 2012); b) A shoal of *Sarpa salpa* (50 mm TL) in a *Posidonia oceanica* seagrass meadow (July 2013); c) A shoal of *D. vulgaris* (30 mm TL) in mixed bottoms composed by sand, gravels, pebbles and rocks (July 2013); d) A group of *D. sargus* in the same habitat (15 mm TL) (May 2013); e) A group of *Symphodus ocellatus* (30-35 mm TL) and one *S. roissali* (50 mm TL) in a *Cystoseira* erect macroalgae forest (September 2012); and f) A *Coris julis* in the same habitat (40 mm TL, September 2012). a-d) depth= 0-1 meters, e-f) depth=2-4 meters. Foreground spans about 0.5-1.5 m wide in each picture. Photos: Adrien Cheminée, Eva Vidal and Amalia Cuadros.

Globally, labrids species settle mainly in slightly deeper areas (3-25 m) than sparids; they are normally found associated with macrophytes, both seagrass meadows or erect algae covering rocky substrates. *Symphodus cinereus* has been reported to settle in *Posidonia* seagrass meadows (García-Rubies and Macpherson, 1995). *Thalassoma pavo* and *Labrus* spp. has been recorded to settle mainly in rocky habitats covered by arborescent erect algae (García-Rubies and Macpherson, 1995). Whereas, juveniles of other *Symphodus* species (*S. ocellatus, S. rostratus, S. roissali, S. tinca*) and *C. julis* appear associated to both seagrass meadows and rocky reefs with macroalgae at similar depths (Bussotti and Guidetti, 2010; Cheminée, 2012; García-Rubies and Macpherson, 1995; Guidetti, 2000; Lejeune, 1984; Thiriet, 2014) (Photo I-3). Moreover, *Labrus* spp. settle in spring, whereas *S. roissali* and *S. tinca* settle at the beginning of summer and *S. ocellatus, S. rostratus, S. cinereus, C. julis* or *T. pavo* settle at the middle or end of summer. Furthermore, species which settle with the same temporality display some degree of spatial partitioning according to depth (e.g. *S. roissali versus S. tinca, C. julis versus T. pavo*) and according to macrophyte features (e.g. macroalgae percent cover) (Biagi et al., 1998; Bussotti and Guidetti, 2010; Cheminée, 2012; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). Additionally, some of the mentioned *Symphodus* species have been reported to settle also in drifting algae or "dead matte" (Cheminée, 2012; Raventos and Macpherson, 2005).

The preferential settlement in a given habitat *versus* others, for each species, has been stated by comparing the juvenile densities of each species in different habitats. However, exhaustive comparisons were done in only a few studies and they are centred in NW Mediterranean Sea (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995).

Furthermore, although we have some bibliography which report where sparid and labrid settlers are more abundant, few is known about associated processes and factors influencing these juveniles' density patterns (Thiriet, 2014). Among processes which may influence these habitat use patterns, growth and survival should be better understood in order to better assess the nursery role of such habitats (Beck et al., 2001).

I.1.4. Driving factors on settlement and post-settlement processes

I.1.4.1. Pre- versus post-settlement processes

For a given nursery habitat (*sensu* Beck et al (2001)) for a given species, although the nursery habitat is present, its nursery value can vary geographically (i.e. between sites). The apparent discrepancy in the importance of nurseries in different regions could be understood, by examining processes and factors that contribute to local variation in the nursery value. The ability of a given habitat to produce juveniles that will be recruited into adult population is shaped by pre- and post- settlement processes which are influenced by driving factors. During pre-settlement phase, various processes may act: the primary one is the effectiveness of the adult reproduction, which is influenced by fish condition and environmental factors such as temperatures and photoperiod (Vlaming, 1972). Then the larval supply to the juvenile habitat is another main pre-settlement process, it is mainly determined by larval survival in the pelagic environment and the structural connectivity between juvenile habitats in relation to the breeding areas. Such structural connectivity is influenced by the hydrodynamism: currents circulation must be coupled with coastal geomorphology where habitat are placed (Roy, 1998). These pre-settlement processes and factors determine the initial density of juveniles supplied to juvenile habitats in a given site.

Hereafter, post-settlement processes and factors influence the nursery value of a given habitat and site. They act within the benthic juvenile habitat. Since fish species in their early juvenile phases are particularly vulnerable (Ware, 1975), the intolerance of physical extremes and the starvation and predation in the habitat are major causes of mortality (Sogard, 1997; Sogard and Olla, 1993). Hall et al. (1997) considered habitat quality as the ability of the environment to provide conditions appropriate for individual and population persistence. A high quality juvenile habitat must provide sufficient refuge and food for a given juvenile species. In this sense, high levels of habitat structuration (i.e. habitat complexity and heterogeneity) seem to increase both shelter and food availability for juveniles. This may facilitate juvenile survival and growth processes, which in turn will make them less vulnerable to predation in the habitat (Behrents, 1987; Connolly, 1994; Dahlgren and Eggleston, 2000; Heck et al., 2003; Hixon and Beets, 1989; Levin, 1994; Schulman, 1984; Tupper and Boutilier, 1997). Habitat transformations induced by human

stressors may modify habitat tri-dimensional structure and subsequent quality in terms of shelter/source of food for juveniles. Furthermore, survival and growth processes within the nurseries may be influenced by others factors, e.g. protection (i.e. no take areas) and consequent higher densities of predators and adults competitors (Arceo et al., 2012; Hereu, 2004; Jones, 1987; Planes et al., 2000; Tupper and Boutilier, 1995; Tupper and Juanes, 1999). Finally, connectivity between juvenile and adult habitats is essential to replenish adult populations (Gillanders et al., 2003; Huijbers et al., 2013).

As a conclusion, such processes and factors have a high influence on the final production of juveniles of a given nursery habitat: understanding processes and factors which consequently shape the nursery value of a given habitat must be studied (Adams et al., 2006; Beck et al., 2001; Manson et al., 2005; Sheaves et al., 2006).

I.1.4.2. Factors threatening nursery habitat availability and quality

Coastal habitats comprise some of the most productive and valued ecosystems of the world (Costanza et al., 1998), notably through the presence of essential habitats such as nurseries. However they are as well the most threatened marine areas worldwide because they are highly influenced by direct human pressures (Halpern et al., 2008). Consequently, the availability and the quality of juvenile habitats are threatened by the different stressors acting in such seascapes. Top human threats to coastal marine ecosystems are the direct destruction (e.g. via coastal engineering); the pollution from toxins or fertilizers from urban, agriculture and aquiculture development; the altered sedimentation by damming, diverting freshwater or tidal influence, the deforestation or land clearing and the overexploitation; additionally they are affected by the products of the globalization such as invasive species and disease; and by the products of global climate change, such as increase of temperatures, rates of sea-level rise, ocean acidification, and UV exposure (Crain et al., 2009).

In the particular case of the Mediterranean Sea, it is one of the most endangered seas of the world due to its historical exploitation, and is suffering important loss of habitat along its coasts (Bianchi and Morri 2000, Coll et al. 2010, Mouillot et al. 2011). The European “Habitats” Directive aims at minimizing impacts on coastal habitats. Such policy insists on improving the knowledge of the habitats which are important for fish life-cycles and insists

in identifying high quality habitats (Ducrotoy and Pullen, 1999; European Commission, 2011).

I.1.4.3. How to identify high quality habitats for juveniles?

To identify high quality habitats in general is difficult worldwide, since rigorous historical baselines worldwide are difficult to obtain or needs more attention by scientist (Sáenz-Arroyo et al., 2006; Schrope, 2006). Furthermore, it is no longer possible to return to past ecosystems equilibriums because an important percentage of both the landscape and seascape has been transformed irreversibly, and many species which in the past had an ecological role (including in marine ecosystems) have disappeared or are in risk of extinction in different regions (Ferretti et al., 2008; Foley et al., 2005; Jackson et al., 2001; Vitousek et al., 1997). In this sense, our only way to identify healthy sea ecosystems at present is through the improvement of our knowledge in Marine reserves. Marine reserves provide us baseline data against which to compare present conditions in other regions and thus to evaluate the abundance of marine species or the structure of marine ecosystems (Dayton et al., 2000; Sala et al., 2012). In this sense, improving the knowledge of juvenile abundances harboured by Marine Protected Areas (MPAs), may provide a baseline data to recognize abundance levels that are typical of healthy ecosystems at present. However the results of protection in juvenile fish are ambiguous (García-Charton et al., 2008; Planes et al., 2000). Furthermore most of the marine protected areas are not designed to protect early life stages or juveniles (Roberts et al., 2001). In spite of this, improvement on the knowledge of nursery habitats of some species has allowed marine managers to begin monitoring juvenile populations and their habitats (Cheminée, 2012; Cheminée et al., 2014) and to design protected areas taking into account early juvenile phases and habitats (Botsford et al., 2003). Improving the knowledge of processes and factors which affect nursery habitats and juveniles are required to allow us to feed future management practices.

I.1.5. Aim of this thesis

The aim of this thesis was to understand in Minorca island the influence of potentially important factors in determining the density distributions and dynamics of labrids and sparids juveniles among their juveniles habitats: seagrass meadows, arborescent

macroalgae forests and mixed bottoms of sand, pebbles and boulders. These factors were: 1) the three-dimensional structure of the environment *sensu lato*, from the large scale coast configuration and depth to the lower scale habitat structure; 2) biological interactions in terms of presence of predators and adult con-specifics; and finally 3) physical constrains in terms of meteorological conditions.

Such influence was studied by the examination of pre-settlement and post-settlement processes for various target species under the contrasted influence of selected driving factors. In chapters II and III we studied the full summer juvenile assemblage (i.e. comparative densities of all taxa) within two nursery habitats: *C. nodosa* meadows and *C. brachycarpa* forests, while the two following chapters focused on *Diplodus sargus* settlement and post-settlement processes in heterogeneous shallow mixed bottoms composed by sand, gravels and pebbles. Every chapter is written to be understandable independently of each other section. More precisely, this thesis has been structured as follow:

-Chapter II focused on the study of the influence of *Cymodocea* meadows habitat structure (i.e. more or less structured through the presence of boulders) on juvenile density patterns at various spatial scales (from <1m, to 10 m, to 1 km).

-Chapter III focused on the understanding of the patterns of juvenile fish densities and species-specific juvenile behavior within *Cystoseira* forests according to three possible drivers: i) habitat structure (i.e. canopy height and cover); ii) depth (considering three depth strata between 0 and 12 meters) and iii) protection levels (comparing no-take *versus* non-protected areas separated from 30 km), taking into account the spatial variability between sites separated by few kilometers.

-Chapter IV analyzed settlement and post-settlement processes of *Diplodus sargus* within its nursery habitat, assessing the arrival of settlers, their growth, mortality rates and recruitment level in relation to environmental variables: hydrodynamics and temperature.

-The objective of Chapter V was to quantify and compare *Diplodus sargus* settlement and post-settlement densities under the influence of contrasted seascape attributes at different spatial scales: coastal localization, cove configuration in terms of exposure levels, and microhabitats features.

-In Chapter VI the results of all chapters were broadly discussed.

-Chapter VII presents the general conclusions of the thesis.

-Chapter VIII provides supplementary data related to some chapters.

I.2. MATERIAL AND METHODS EMPLOYED IN THIS THESIS

I.2.1. Study Area, preliminary exploration, studied species and habitats

I.2.1.1. Study area: Minorca island

The different samplings of this PhD thesis were conducted through the coasts of Minorca island, in the Western Mediterranean sea. It is a West-East elongated island approximately 44 and 17 km long and wide respectively. It is the easternmost and northernmost island of the Balearic Archipelago, located 39°47' to 40°00'N and 03°52' to 04°24'E (Fig. I-7). Minorca is characterized by the good quality status of its ecosystems. In fact it was declared “Biosphere Reserve” in 1989 (UNESCO, n.d.). Almost all of its coasts have been classified amongst the special status of the European Union classification system for exceptional natural habitats; under the Spanish jurisdiction they are therefore declared LICs (“Lugar de Interés Comunitario”, i.e. “SCI”: Site of Community Importance) and/or ZEPAs (“Zona de Especial Protection para las Aves”, i.e. “IBA”: Important Bird Areas) (Fig. I-3). Furthermore, the Marine Protected Area (MPA) “Reserva Marina del Nord de Menorca” was established in 1999 in the northern coast of Minorca (Fig. I-3); it covers 5119 ha and most of it is classified as partial reserve, as some fishing is still allowed (Coll et al., 2012), and no take-areas cover only 1055 ha (Fig. I-3). Smooth reliefs dominate the island, and it display a contrasted north *versus* south landscape due to its geology (Fig. I-4). North landscape is mainly shaped by mixed metamorphic substratum, resulting in small hills and wide and shallow valleys. South landscape is made of carbonate substratum, and as a consequence the south part of the island has many small ravines (Sanuy and Díaz, 2002) and displays karstic erosive systems (Photo I-4). Both northern and southern coasts are characterized by the presence of numerous coves (i.e. 101 in total) interspersed along the shoreline.

Photo I-4. Minorca island landscapes: a-b) Small hills and wide and shallow valleys dominate the north island landscape; c-d) small ravines and karstic erosive systems dominate the south island landscape. Photos: Adrien Cheminée

The climate of Minorca is typically Mediterranean, with warm average temperatures and seasonal rainfall regime. The most remarkable climatic phenomenon of Minorca is the "Tramontana", a dry and virulent wind from the north-west, especially blowing at winter (Llompart et al., 1979).

The Infralittoral of Minorca is dominated by seagrass meadows composed by *P. oceanica*. In areas protected from rough hydrodynamics, e.g. in the Fornells Bay or the Port of Maó, *C. nodosa* seagrass meadows are also present. The rocky reefs with photophilic macro-algae, less abundant than seagrass meadows, are mainly present at the north of the island (Fig. I-5).

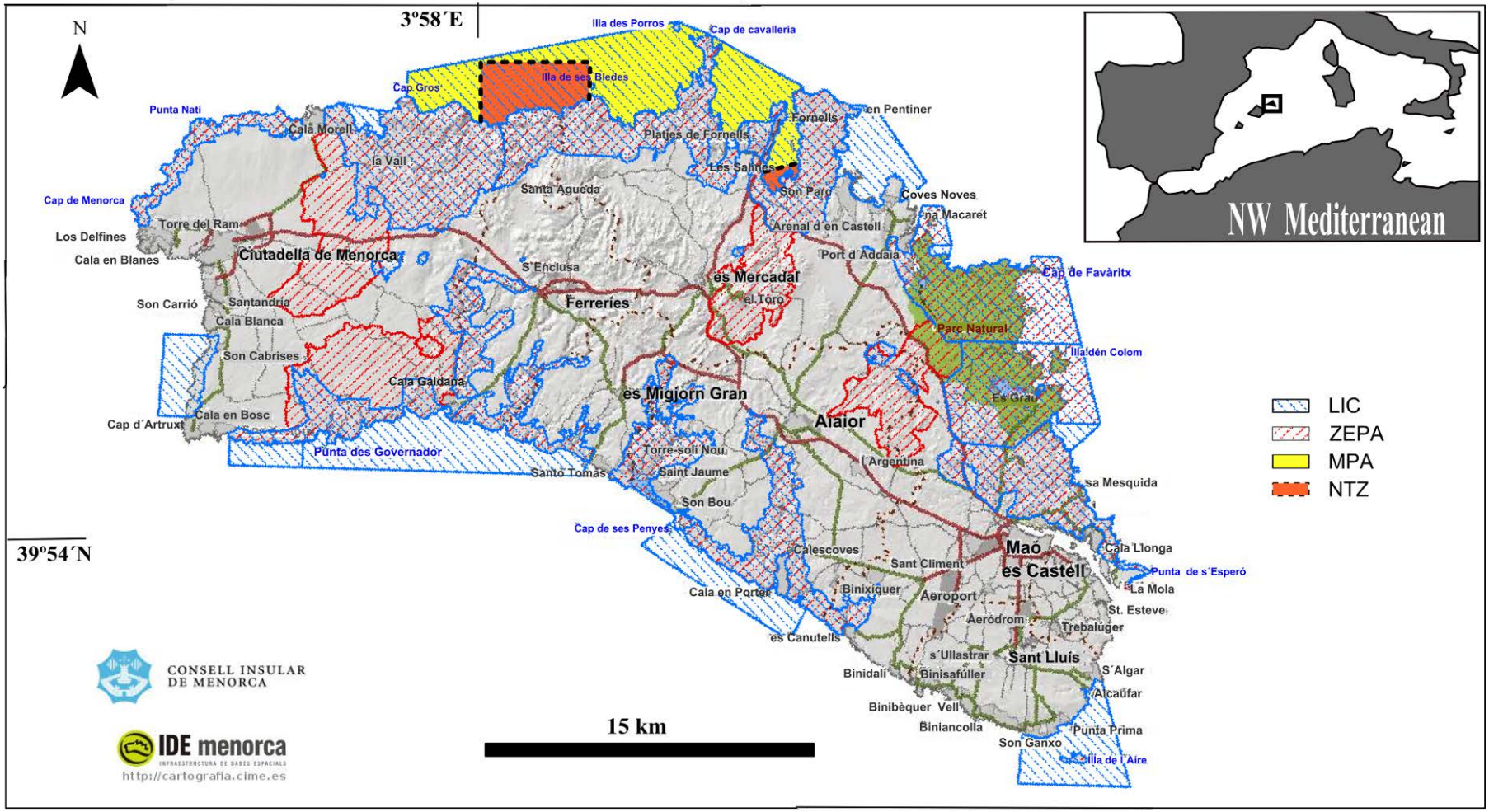

Fig. I-3. Special status of the coasts and lands of Minorca island. Marine Protected Area (MPA) "Reserva Marina del Nord de Menorca", no take zones (NTZ) inside the MPA, LICs (= "SCI" : Site of Community Importance) and ZEPAs (= "IBA", Important Bird Areas) of the Island. Source: Visor IDE Menorca (Silme s.a., 2015).

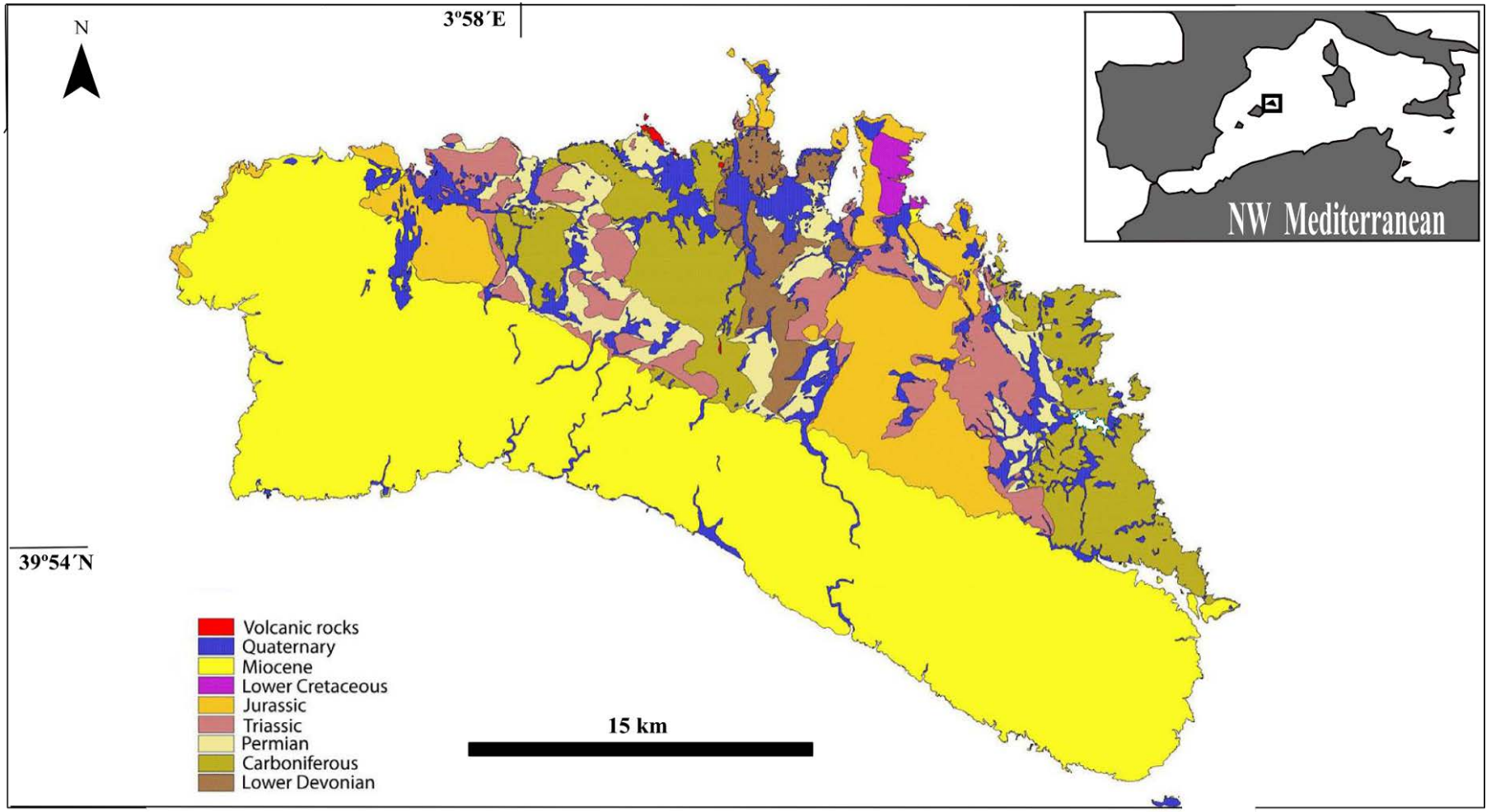

Fig. I-4. Simplified geological map of Minorca island: the northern part of the island is mainly composed of Palaeozoic and Mesozoic mixed metamorphic rocks while Tertiary carbonate rocks are found in the southern region (Andreetta, 2009; Rosell and Llompart, 2002).

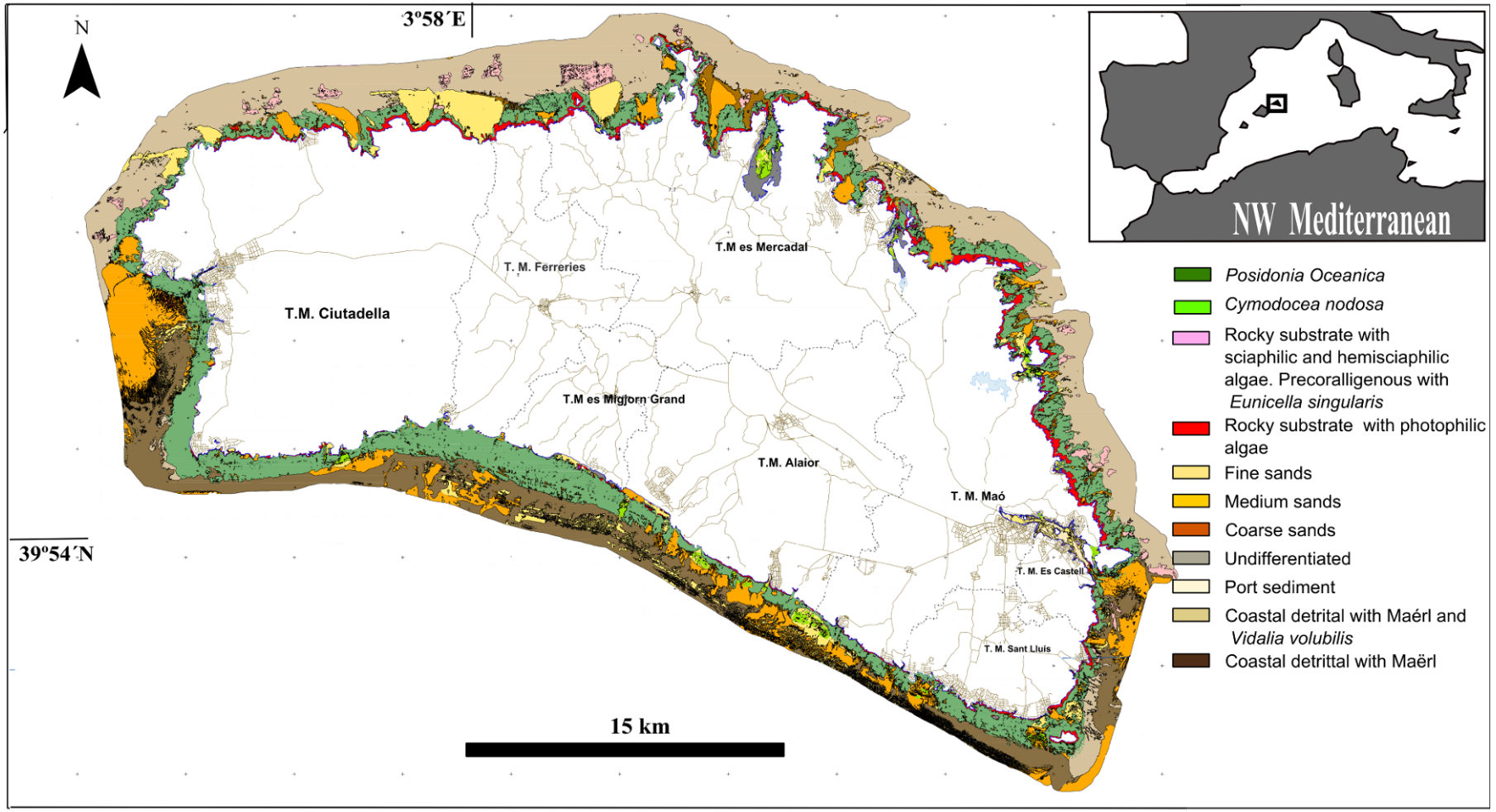

Fig. I-5. Marine biocenosis of Minorca island. The infralittoral is dominated by *Posidonia oceanica* meadows. Modified from: U.T.E. Intecsa-Inarsa, s.a., (2008).

I.2.1.2. Preliminary exploration of juvenile habitats

Juvenile fish have been poorly studied at Minorca island until recently, apart from a few studies (Cardona, 1999; Thiriet, 2014). Consequently we accomplished a preliminary exploratory survey of thirty coves (~30% of Minorca island coves) at the beginning of this thesis in summer 2011 (June 10th - 20th 2011). This exploratory survey allowed us to identify shallow habitats and juvenile species present at Minorca island, as well as to identify some possible driving factors that may act on juvenile density patterns distributions. Preliminary results of this pilot study (unpublished data) indicated high spatial variability in the juvenile assemblages between sites spread around the island. The most abundant juveniles species belonged to the sparids, especially *D. sargus*. Other juveniles were also abundant but belonged to species which typically forms multitudinous shoals (Atherinidae, Mugilidae). Labrids were also present (Fig. I-6).

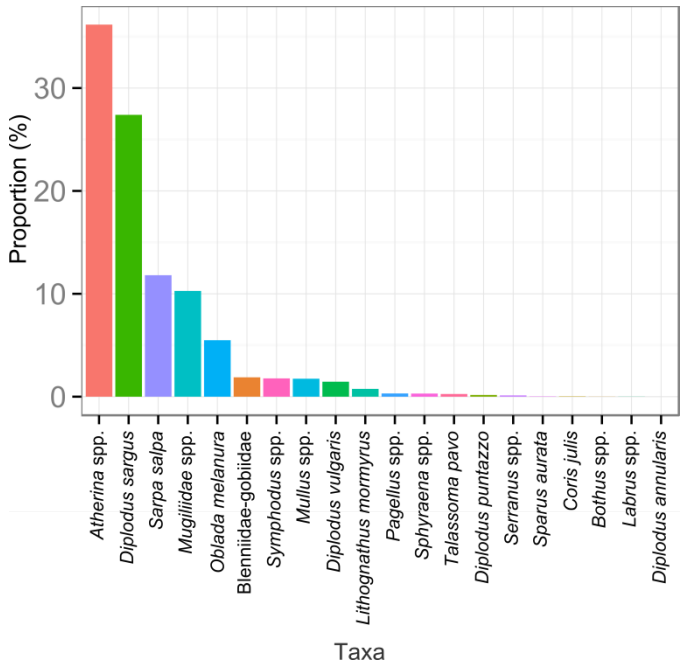

Fig. I-6. Proportion of juveniles fish taxa recorded during the preliminary study accomplished in thirty coves of Minorca island

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Juvenile densities for various taxa varied according to habitats types within coves (personal observation), but as well according to cove orientation (north *vs*. south) and exposure level (Miller, 1985), human settlements and categories of use of coves by bathers (Juaneda and Roig, 2002). Indeed, richness increased for sites with human settlements or which were intensively used by bathers. These areas although impacted,

still have a good water quality (Sales, 2010). In these areas we observed juveniles of species typical of two types of water quality: pristine, with juvenile Labridae, *versus* harbor waters, with notably juveniles of Mugilidae. However, the influence of such factors (positive, negative or not influence) depended on the species and sometimes varied spatially (personal unpublished data).

Furthermore, this pilot study allowed us to identify and localize *in situ* some of the dominant habitats at shallow depths: *C. nodosa* seagrass meadows, *C. brachycarpa* forests and heterogeneous shallow mixed bottoms composed by sand, gravels and pebbles. Consequently, this pilot study enabled us to select the different regions and sites for our study designs (Fig. I-7). More particularly, it enabled us to take into account the possible influence of orientation, exposure, and water quality for avoiding sampling biases and selecting homogeneous sites in each chapter.

I.2.1.1. Studied sites, associated habitats and juvenile species

For each chapter, studied sites and corresponding habitats and species were (Fig. I-7):

-Chapter II: Fornells Bay, located in the north of the island of Minorca, is part of the MPA "Reserva Marina del Nord de Menorca". In this bay extensive *C. nodosa* meadows cover the bottom. We studied the whole juvenile fish assemblage associated to these meadows.

-Chapter III: "Reserva Marina del Nord de Menorca" and adjacent un-protected north coastal areas. The rocky Infralittoral of the northern coast of the island is covered by extensive *Cystoseira brachycarpa* forests; conversely such habitats are scarce along the south coast (Sales, 2010). We studied the whole juvenile assemblages associated to such forests.

-Chapter IV: two groups of coves with shallow bottoms dominated by a mix of sand, pebbles and rocks, and with similar configuration in terms of exposure and water quality were selected. One group of coves was placed at northeast, and the other at southwest. In these sites we studied the juveniles of *Diplodus sargus*.

-Chapter V: we selected twelve coves widespread around the island, with shallow bottoms dominated by a mix of sand, pebbles and rocks, with similar water quality, and

with two possible configuration in terms of exposure. In these sites we studied the juveniles of *Diplodus sargus*.

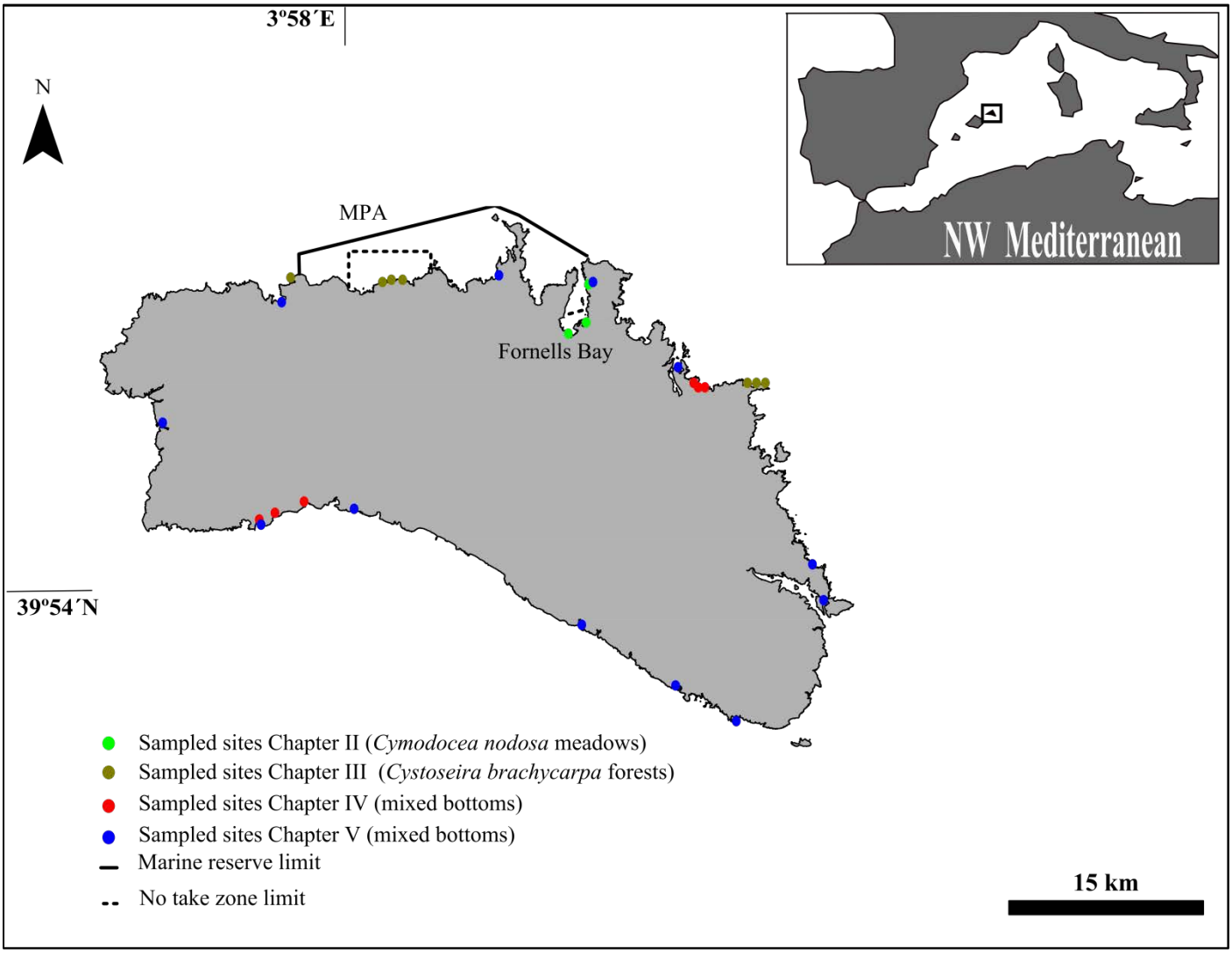

Fig. I-7. The sampled sites of the different chapters of this thesis. Chapter II samplings were accomplished in *Cymodocea nodosa* meadows placed in Fornells Bay, Chapter III in *Cystoseira brachycarpa* forests placed in the MPA and through the north coast of the island, and samplings of Chapter IV and V were carried out in mixed bottoms of sand, pebbles, gravels and rocks both at north or south parts of the island.

I.2.2. Collection data methods

Field surveys were conducted during the warmer months (from April to October) during three years from 2011 to 2013. This sampling period coincides with the presence within nursery habitats of juveniles of many Mediterranean littoral fish species (Biagi et al., 1998; Bussotti and Guidetti, 2010; Félix-Hackradt et al., 2013a; García-Rubies and Macpherson, 1995) (Fig. I-2).

For each chapter, abundance and size of juveniles were assessed by means of Underwater Visual Census (UVC) (Harmelin-Vivien et al., 1985) (Photo I-5). At each site, fish were counted and their size estimated during daylight (between 9 am and 4 pm), by the same previously inter-calibrated and trained observers. The total length (TL) of individuals was estimated with the help of fish silhouettes of different sizes (5 mm TL size-classes) on a plastic slate (Macpherson, 1998). Additionally, in Chapter III, behavior of fish were recorded (i.e. interaction type of fish with substratum, see details in this chapter). In each chapter, the area of the sampling units (replicates) was adapted to the characteristics of the habitat and the specific objectives of the study (see details in each chapter). In Chapter II and III, replicates were haphazardly selected by the diver during a preliminary exploration in each study site and located by a small mark. In Chapter II, to study the influence of habitat structure (through the presence of small boulders) at two different scales among a seagrass meadow, we employed random replicate belt-transects of 6 m x 3 m and random point-counts on 25 cm x 25 cm plots. At each point-count, the diver visualized an imaginary plot were abundances and TL of juvenile fishes were recorded during 5 minutes (Cheminée et al., 2013; Francour and Le Direac'h, 1994; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1985). In this chapter, all census were accomplished at depths ≤ 1 m and snorkelling equipment was employed. In order to record juveniles behaviors at different depths in Chapter III, 5 minutes-counts in imaginary plots of 1 m^2 were accomplished by SCUBA divers at the three depth range considered: d1 (3-5 m), d2 (6-8 m), and d3 (10-12 m) (Cheminée et al., 2013; Francour and Le Direac'h, 1994; García-Rubies and Macpherson, 1995). In Chapter III the effect of protection was measured in terms of abundances, sizes and biomass of adult con-specific and predators. For that, we performed UVC recording their abundance and TL (±1cm) at each site and each depth strata in three replicate belt

transects of 10 m x 6 m (Harmelin-Vivien et al., 1985). Chapter IV and V focused on the temporal patterns of *D. sargus* juveniles densities, which use the mixed bottoms of the shallow part of coves as nursery; they distribute near the surface; consequently, census were accomplished by snorkelling along pre-defined transects running parallel to the shoreline (55 meters mean length) and covering the entire cove. The beginning and end of each transect were referred to some physical features of the topography of the coastline, to ensure accurate repeatability overtime independent of the observer. Such transects were placed at depths ranging from 0.5 to 3 m.

Furthermore, in Chapters II, III and V, habitat descriptors were recorded with the aim to take into account habitat structure. In Chapters II and III, the structure of macrophyte-formed habitat was described through macrophytes descriptors. We measured for each of the dominant macrophytes their percent coverage and maximum height (to the nearest cm) (Cheminée, 2012) ; this allowed us as well to describe the macrophyte composition when various macrophytes were present among the meadows (Chapter II). In Chapter V micro-habitat structure was described, differentiating transects according to the substrate type of the bottoms in terms of dominance of sand *versus* rocky substratum or mixed substratum of sand and rocks; furthermore depth was visually estimated for each kind of substratum.

Other environmental parameters were obtained by different ways. In Chapter IV hydrodynamism data were provided by *Puertos del Estado* (Puertos del Estado, 2015) by its monitoring at two buoys. Meanwhile temperatures were recorded by Onset HOBO Water Temp Pro v2 sensors placed on the bottom at 5 m depth in each site. In Chapter V, exposure of coves was measured using Miller index (Miller, 1985). See further details and sampling designs in each chapter.

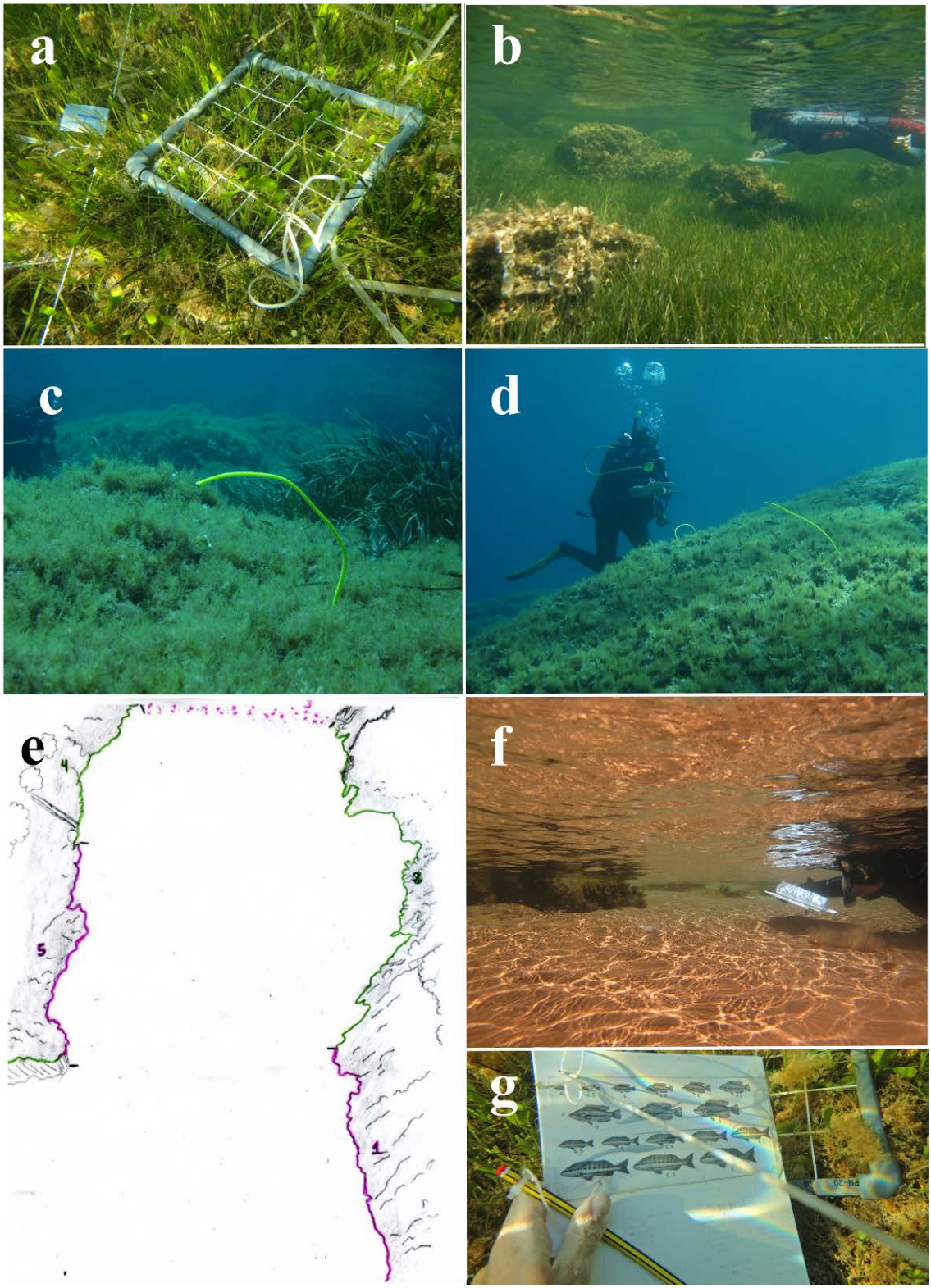

Photo I-5. Sampling methodology of this thesis: a-b) we used UVC belt-transects for fish counts and 50 cm x 50 cm quadrates for canopy descriptions in *Cymodocea nodosa* meadows (Chapter II); c-d) 5 minutes UVC in imaginary plots of 1 m² were accomplished in *Cystoseira* forests (Chapter III); e-f) UVC in pre-defined transects running parallel to the shoreline were employed in mixed bottoms of sand, pebbles and boulders (Chapters IV-V). Coves were mapped in order to delimitate each transects; g) fish silhouettes in a plastic slate to estimate TL of each observed fish. Photos: Adrien Cheminée, Eva Vidal, Jaime Sintes and Amalia Cuadros.

I.2.3. Data treatment and statistical analyses

In Chapters II and III, for each taxa, every observed individual smaller than one third of adult maximum total length (Cheminée, 2012; Louisy, 2002) were considered for the juvenile analyses. In Chapters IV and V a given juvenile cohort was followed through time. In Chapters II and III density data were standardized to 1 m^2 for further comparisons (Thiriet, 2014). Whereas for the chapters IV and V, where counts were made parallel to the shoreline, fish densities were standardised to one linear meter of shoreline (Cheminee et al., 2011; Harmelin-Vivien et al., 1985).

Statistical analyses were made using different descriptive, exploratory and inferential approaches. The main methods used to describe data were numerical tables, percentages and the graphical representations: boxplots, barplots and smooth curves (see further details in each chapter). The main exploratory analyses consisted in ordination methods. We used Multidimensional Scaling (MDS): nMDS (non-metric Multi-Dimensional Scaling) and PCO (Principal Co-ordinates Analysis). Such methods allow us to project the data on a vector space, in order to have a visual representation of "closeness" (similarity) of the samples and allow us visualize the relationships between samples. nMDS is based on the relationships between ranks of dissimilarities and distances among samples. Which is very proper to ecological data since relationships on biological data are often non-linear (Anderson and Gorley, 2008; Clarke and Gorley, 2006). nMDS were used to represent fish assemblages in Chapter II and III, and to represent habitat descriptors in Chapter II. However nMDS routines represent the points without trying to represent it better according to a specific factor. The PCO, also known as metric MDS, allow to represent samples according to selected factors (Anderson and Gorley, 2008). It was a better model to represent juvenile assemblages in Chapter II, since nMDS didn’t produced clear representations according to our factors of interest. Such methods work on objects rather than variables and give us only the representation of the samples. In Chapter III a PCA was employed in order to obtain a new variable (i.e. PC1 axis) as a single descriptor of the forest three-dimensional structure, because such analysis is based in variables (rather than in objects), allowing us to obtain a set of values (new variable) from the relationship established between the original variables (Anderson and Gorley, 2008; Clarke and Warwick, 1994; Fielding, 2015).

When convincing ordination of samples were obtained in the juvenile assemblages plots, individual species contributions to the separation of samples' groups were examined by SIMPER (Similarity percentage breakdown) routines (Chapter III) (Anderson and Gorley, 2008; Clarke and Warwick, 1994).

In complement to exploratory approaches, patterns and putative differences between groups were tested through inferential approaches. This was performed by using univariate and multivariate PERMutational Analyses Of Variance (PERMANOVA), which *p*-values are based on random permutations of the data, ignoring the factors being tested and thus such analyses are very powerful and flexible; it allows determining the influence of the factors of interest (Anderson and Gorley, 2008). Such analyses were made in Chapter II, III and V, in order to test the variation of the response variables according to our factors of interest; uni- and multi-variate response variables included: juvenile density (Chapter II, III and V), juvenile TL and juvenile behavior (Chapter III). PERMANOVA models were factorial, nested or crossed (see such models detailed in each chapter).

Both exploratory and inferential approaches are based on the concept of resemblances between samples. Various indexes (distances, similarities or dissimilarities) are available in the literature to measure such resemblance and the choice relies on the nature of the data (Anderson and Gorley, 2008). The nMDS and multivariate PERMANOVAs were constructed based on Binomial deviance (scaled) resemblance measures. It emphasizes on species composition under null hypothesis that the compared communities are equal. It is theoretically able to handle variable sample sizes (Anderson and Millar, 2004). PCO was constructed based on Modified Gower distances, since the previous measure of dissimilarity didn't display clear patterns in the plots since binomial measures may not be able to properly handle samples with no shared species. Modified Gower distances smoothly weights (e.g. log base 2) abundance information (Anderson et al., 2006). PERMANOVA on multivariate contingence tables of behavior were analyzed using Sogard resemblance matrix, which is a non-parametric alternative to the Chi-squared measure of distance (Clarke and Warwick, 2001). Euclidean distance measures were employed for univariate PERMANOVA analyses (Anderson and Gorley, 2008). SIMPER analysis routines are based on the use of Bray-Curtis resemblance matrix.

Furthermore, in Chapters IV and V, ANCOVAS, which blends ANOVAs and regressions (Ellison and Gotelli, 2004), were employed to evaluate whether juvenile density or growth means were equal across levels of the categorical independent variable (e.g. “coves”) while statistically controlling for the effects of the covariate “time” (Ellison and Gotelli, 2004). Additionally, in Chapter IV, other inferential regression methods were employed: VIF (variance inflation factor), linear models and Spearman correlations. VIF was employed to quantify the increase of the variance of the coefficients of the regressions of hydrological and temperature data through time, in response to the multicollinearity among these environmental variables (Lin et al., 2012). These methods allow us to select not correlated environmental variables for further analyses. Among linear models used in this chapter, General Additive Model (GAM) analyses were employed to obtain the relationship among the selected environmental variables and the mean density or growth of juveniles. GAMs, which are a nonparametric extension of Generalized Linear Models (GLMs), were used because we haven’t a priori reasons for choosing a particular response function, and such strategy allow us to obtain the best adjusted modality functions (Guisan et al., 2002; Hastie and Tibshirani, 1990; Wood, 2003). Simple linear regressions were employed to obtain density or growth rates of *D. sargus*. Finally the non-parametric Spearman rank correlations were employed to additionally test correlation among VIF-selected environmental variables in Chapter IV. It was also employed in Chapter III to test possible correlations between *Cystoseria* height and cover, and as well in the nMDS and PCO plots of Chapter II and III, to superimpose arrows representing the correlations between biplot axes and variables.

The methods used along this thesis were mainly non parametric (nMDS, PERMANOVAS, GAMs, Spearman rank correlations) and thus normality and homosedactisity of data were not strictly required. However, when data contained species much more abundant than others multivariate analyses were performed on transformed data (square root). When other routines were employed (PCA, PCO, linear models) data were explored in order to test its normality and homoscedasticity and were transformed if required.

Exploratory analyses and inferential tests were performed using the PRIMER 6 and PERMANOVA + B20 package (Anderson and Gorley, 2008; Clarke and Gorley, 2006),

and “mgcv” package in R Environment (R Development Core Team, 2013). Graphical visualizations were also performed in R Environment using the library ggplot2 (Wickham, 2009).

Chapter II. Effect of the three-dimensional structure of *Cymodocea nodosa* meadows on Mediterranean juvenile fish assemblages: the role of spatial scale

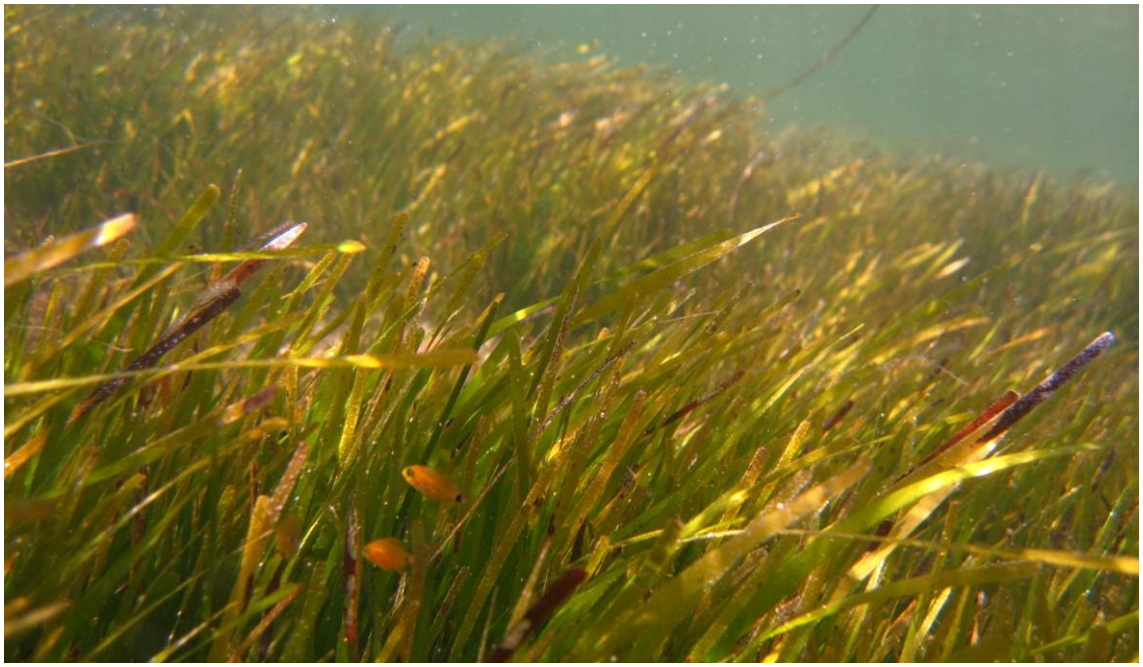

Photo II-1. *Cymodocea nodosa* meadows in Minorca island , depth = 1 meter, July 2012. Foreground spans around 0.3 m wide. Photo: Amalia Cuadros.

This chapter will be adapted and submitted in 2015 to an international journal (Journal of Experimental Marine Biology and Ecology – 5YIF 2.3), with the co-authors as follow:

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Chapter II. Effect of the three-dimensional structure of *Cymodocea nodosa* meadows on Mediterranean juvenile fish assemblages: the role of spatial scale

II.1. INTRODUCTION

II.1.1. Context of the study

Seagrass meadows have declined worldwide as a result of human stressors, mainly the increase of nutrients and sediments runoff, the presence of invasive species, hydrological alterations, commercial fishing and global climate change (Delgado et al., 1997; Duarte, 2002; Orth et al., 2006; Waycott et al., 2009). Seagrass losses are a matter of concern, since seagrass meadows serve many important socio-ecological functions in coastal waters and play an important role in marine ecosystems worldwide (Bertelli and Unsworth, 2014; Bjork et al., 2008; de la Torre-Castro and Rönnbäck, 2004; Jackson et al., 2015; McArthur and Boland, 2006). Seagrasses are considered foundation species (Dayton, 1972) and have an extremely high primary and secondary production rates (Balata et al., 2007; Borowitzka et al., 1990; Pergent et al., 1994; Pergent-Martini et al., 1994; Sánchez-Jerez et al., 1999). In comparison with others marine habitats, seagrass meadows are characterized by a high degree of habitat structuration. Habitat structure is defined as the amount, composition and three-dimensional arrangement of structural components (both abiotic and biotic matter) at a location under a determinate spatio-temporal scale (Beck, 2000; Bell et al., 1991; Byrne, 2007). They are therefore considered as habitat-formers: these meadows support a great abundance and diversity of organisms, including commercially and recreationally important fishery species (de la Torre-Castro and Rönnbäck, 2004; Guidetti and Bussotti, 2002; Pollard, 1984). Seagrasses are also essential for some threatened megafauna species such as sea turtles, dugongs and manatees, and other species of conservation concern, such as seahorses or pipefishes (Hughes et al., 2008).

Many authors have highlighted the nursery role of seagrass meadows for many fishes, due to their higher production of juveniles per unit of surface (nursery value, *sensu* Beck et al. 2001), as compared to less structured habitats, i.e., unvegetated bottoms (Beck et al., 2001; Heck et al., 2003; Pollard, 1984). Furthermore, it has been observed higher juvenile abundances within seagrass meadows, compared to less structurally complex macrophyte meadows, such as *C. prolifera* (Chlorophyta) meadows (Verdiell-Cubedo et al., 2007). However, when comparing seagrass meadows with other structured habitats, such as mangroves, coral reefs, or rocky–algal reefs, all of them display high density of juveniles, with some species-specific variations (Guidetti, 2000; Nagelkerken et al., 2000). The positive correlation between habitat three-dimensional structure and juvenile fish density is probably due to the higher availability of food and/or shelter in structurally complex habitats (Thiriet et al., 2014; Verwey et al., 2006).

Additionally, among a given meadow, it is reported a spatial variability of the meadow three-dimensional structure (Bell and Westoby, 1986a; Guidetti and Bussotti, 2000; Gullström et al., 2008). The meadow three-dimensional structure is the spatial arrangements of its structural components. It has been quantified notably through the measure of the vertical stratification of macrophytes (presence and height of the canopy) and the horizontal distribution of macrophytes (e.g. shoots density, % cover, patchiness) (August, 1983; García-Charton et al., 2004; Guidetti and Bussotti, 2002; Wilson et al., 2007). Within seagrass meadows, the density of juvenile fishes has been reported to be correlated with the height and/or the density of seagrass shoots and the patchiness of the meadow (Bell and Westoby, 1986a; Guidetti and Bussotti, 2000; Gullström et al., 2008). More particularly, the presence of abiotic structures among the meadow (such as intermingled boulders) may have an influence, as illustrated by studies among macro-algae meadows (Cheminée et al., in press). However, the actual relationship between juvenile density and meadow structure is species-specific, since some species display life-strategies (e.g. anti-predator or foraging tactics) adapted to more structured meadows, whereas others prefer less structured ones or even opened areas adjacent to their edges (Horinouchi, 2007). Furthermore there are fishes whose densities are not influenced by seagrass meadow structure, such species are habitat generalist, residents or transients (Horinouchi, 2007; Orth et al., 1984). Additionally, the influence of the meadow structure on juvenile density may depend on the scales of study. Indeed, Bell and Westoby (1986a) found that leaf height and density have a significant effects on

juvenile densities among beds, but few effects between separated beds (>1-10 km apart). Similar results have been reported for other fish species inhabiting other structured habitats formed by other foundation species (Anderson and Millar, 2004). This bibliography supports the importance of the chosen study scales when assessing the influence of habitat structure on fish assemblages. The appropriate scale will depend on the behaviour and displacement capabilities of the studied organism (Beck, 2000; Bell et al., 1991; Byrne, 2007). In the case of juvenile necto-benthic fishes, microhabitats (i.e., habitats which are small or limited in extent and which characteristics differ from surrounding habitats) are thought to significantly influence juveniles' assemblages (Harmelin-Vivien et al., 1995). However, the actual scale of this interaction is still unknown, since data about the mobility of juvenile fishes are scanty (Calò et al., 2013) and since it seems to be taxa- and size-dependent (Vigliola and Harmelin-Vivien, 2001).

Cymodocea is a genus of seagrasses spread from the eastern Atlantic to the western Pacific Ocean (Guiry and Guiry, 2015). *Cymodocea nodosa* (Ucria) Ascherson 1870 is a very common seagrass in shallow (i.e. 0 to 20 meters) and sheltered to semi-exposed, marine, polyhaline or hypersaline water masses of the Mediterranean and western Africa (Borum et al., 2004; Guiry and Guiry, 2015; Mascaro et al., 2009), where it forms mono-specific or mixed meadows with *Posidonia oceanica*, *Zostera noltii* or *Caulerpa prolifera* over sandy-muddy bottoms. As highly resilient species (Malta et al., 2006), it is considered as good indicator of water quality, since it displays faster responses to environmental changes or to anthropogenic stressors than other seagrasses (Olesen et al., 2002; Orfanidis et al., 2010). Due to its resilience, *C. nodosa* is still being considered under the category "Least Concern" for the International Union for the Conservation of Nature (IUCN) Red List, and its populations are still being considered stable (Short et al., 2011). However their populations has been recorded to suffer regressions in some localities (Ceccherelli and Cinelli, 1997; Delgado et al., 1997).

Information about the juvenile fishes inhabiting *C. nodosa* meadows is scarce, but underlines their potentially high nursery value (Espino et al., 2011; Guidetti and Bussotti, 2002, 2000; Verdiell-Cubedo et al., 2007). Furthermore, *C. nodosa* meadows display a variable three-dimensional structure among its meadows; it is due for example to variable meadow shoot density (Barbera et al., 2005), and more particularly, to the

presence of intermingled boulders among *C. nodosa*, resulting in heterogeneous portions in the meadow. Boulders are usually located in the fringe close from the meso and supralittoral, where geological material inputs occur. In this context, there are no studies addressing the influence of *C. nodosa* meadow structure on the juvenile fish assemblage.

II.1.2. Objectives of Chapter II

In this chapter we aimed to study the influence of habitat structure within *C. nodosa* meadows on the assemblage of juvenile fishes at different spatial scales. First, at seascape scale (tens of meters square), we aimed to compare juvenile assemblages between shallow (0.5 - 1 meter depth) heterogeneous portions of the meadows, i.e. scattered with boulders, *versus* homogeneous portions of the meadows, i.e. without boulders. Secondly, at lower scale (< $1m^2$), within the heterogeneous portions of the meadows, we investigated the influence on juvenile assemblages structure of different microhabitats types: i) microhabitats with only *C. nodosa*; ii) microhabitats of *C. nodosa* with a boulder covered with structured, erected and perennial macroalgae (*Cystoseira* spp.); and iii) microhabitats of *C. nodosa* with a boulder covered with less structured and seasonal macrophytes (e.g. Dictyotales and Sphacelariales).

II.2. MATERIAL AND METHODS

II.2.1. Studied area

The study was conducted in Fornells bay, located in the northern coast of Menorca island (Balearic Archipelago) (Fig. II-2). It is part of the marine protected area “Reserva del Nord de Menorca”(Coll et al., 2012). Previous works suggested that Fornells bay may be a settlement and recruitment area for many fishes (Manent and Abella, 2005). The bay is semi-enclosed, 4.4 km long, 1.5 km wide and with an average depth of 5.5 m. It is connected to the Mediterranean Sea by a 300 m wide strait opened towards the north. Benthic communities are characterized by dense meadows dominated by the

seagrasses *Posidonia oceanica* and *Cymodocea nodosa;* although some green macroalgae (Chlorobionta) such as *Halimeda tuna*, *Caulerpa prolifera*, *Dasycladus vermicularis*, and *Flabellia petiolata*, are scattered within the meadows (Delgado et al., 1997). The extensive areas of *Cymodocea nodosa* meadows thrive from 0 to 10 meters depth (Photos II-1 and II-2). In some portions of the meadows, boulders (sizing about 15 cm x 15 cm -20 cm x 20 cm) are scattered within the *C. nodosa* meadows. Boulders are covered (about 60%) by perennial Fucales, mainly *Cystoseira* spp., or alternatively by shorter (< 3 cm tall), shrubby, seasonal macroalgae from the orders Dictyotales and Sphacelariales.

II.2.2. Sampling design

Sites were selected after a broad exploration of Fornells bay. In order to avoid possible confounding effects between our study variables and other environmental variables, the selected sites were similar in terms of depth (0.5 – 1 m) and slope (<15 º). We defined two types of meadow structure and three types of microhabitats. Among the meadow, the two types of meadow structure were defined and attributed to meadow portions, sizing several tens of meters square. They were: i) heterogeneous meadow portions (i.e where sparse boulders occupy 20-40 % cover of the total meadow area) or ii) homogeneous meadow portions (without boulders) (Photo II-2). Meadow structure was described by recording the percent cover of boulders and macrophytes and the maximum height (to the nearest cm) of the habitat components (i.e. boulders, seagrass and algae canopy) within the replicates were censuses were carried out (see below) (Cheminée, 2012) (see Table II-1).

Photo II-2. The two defined types of meadow structure within the *Cymodocea nodosa* meadows: a) heterogeneous seagrass portions, with 20-40 % of boulders in the meadow; b) homogenous seagrass portions, without boulders in the meadow. Depth = 1 meter, July 2013. Foreground spans around 1.0 m wide in each photo. Photos: Jaime Sintes.

Secondly, various types of microhabitats (25 cm x 25 cm) were defined within the heterogeneous portions of the meadow (Fig. II-1): "cn": *Cymodocea* meadow (25 cm x 25 cm) without boulder; "cy": *Cymodocea* with a boulder mostly covered (60%) by *Cystoseira* spp. (5-15 cm height); "sh": *Cymodocea* with a boulder mostly covered (60%) by shrubby algae (<3 cm height). This two different design, at two different spatial scales (i.e. meadow portions and microhabitat types) were replicated at 3 random sites within Fornells bay (sites S1, S2 and S3 (Fig. II-2)).

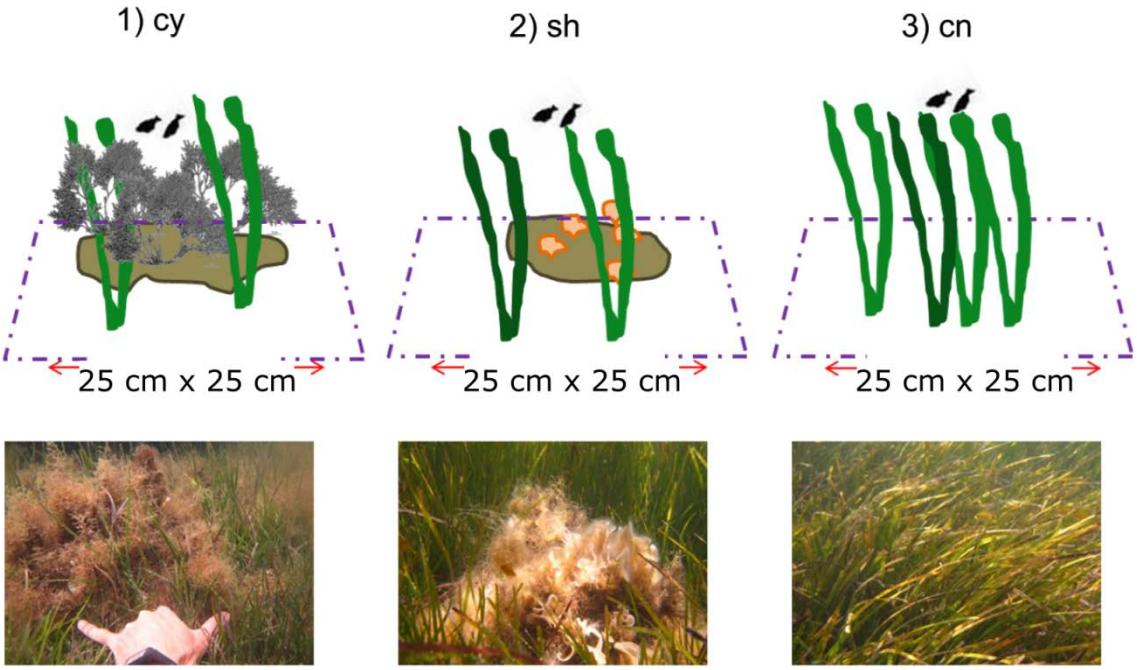

Fig. II-1. The three types of microhabitats sampled within heterogeneous portions of the *Cymodocea nodos*a meadows (25 cm x 25 cm): 1) cy: meadow microhabitats with a boulder mostly covered with *Cystoseira* spp. (5-15 cm height); 2) sh: meadow microhabitats with a boulder mostly covered with shrubby algae (<3 cm height); 3) cn: meadow microhabitats without boulders.

Juvenile fish assemblages associated to *C. nodosa* meadows were sampled in three consecutive years (2011, 2012 and 2013). Surveys conducted in 2011 and 2012 aimed to test the putative effects on juveniles of the various microhabitat types within the heterogeneous meadow portions, in two sampling months (July *vs.* September). Conversely, surveys conducted in 2013 aimed to test the putative effects of different types of meadow structure (homogenous vs. heterogeneous) within the same meadow and sampling months (July *vs*. September).

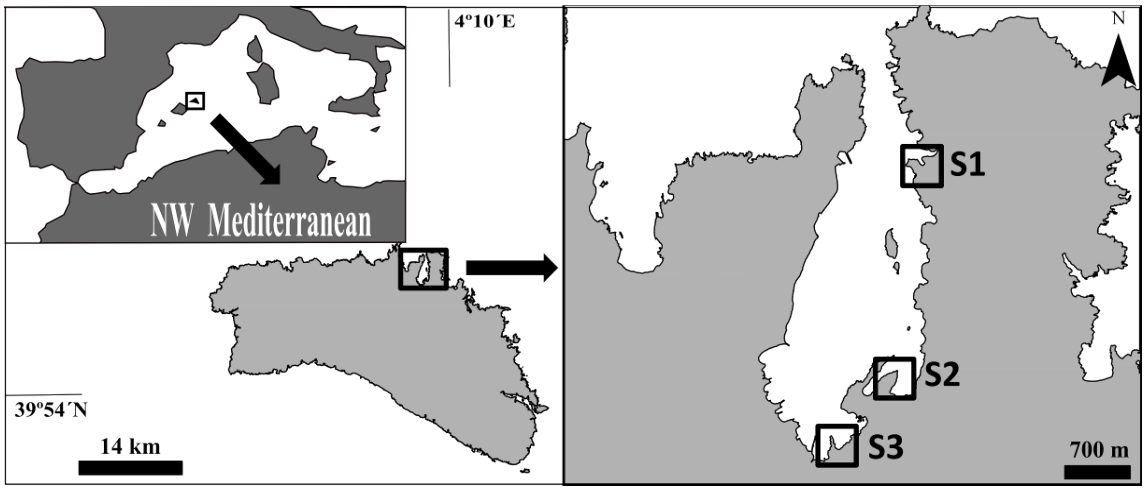

Fig. II-2. Location in Fornells bay (Minorca) of the three surveyed sites of Chapter II. Sites were: S1 (40° 1'52.17" N, 4° 7'22.14" E), S2 (40°02'3.41" N, 4°08'15.66" E), and S3 (40°01'52.17" N, 4°7'22.14" E).

II.2.3. Data collection

During each sampling year (2011, 2012 and 2013), we sampled 2 times, July (between 13th and 29th July) and September (between 9th and 23th September). These two sampling months coincides with high occurrences within the meadow of juveniles of many Mediterranean littoral fish species (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995).

Fish juvenile assemblages were surveyed by means of underwater visual censuses (UVC) techniques (Harmelin-Vivien et al., 1985). For each taxa, all individuals smaller than one third of adult maximum total length (Cheminée, 2012; Louisy, 2002) were considered as juveniles. Abundance and total length (TL) of juvenile fish were recorded during daylight (between 9 am and 4 pm) and moderate and rough sea states, as well as poor visibility days, were avoided. Census were carried out by three previously inter-calibrated divers, using snorkels, and the TL of juveniles was estimated with the help of

fish silhouettes of different sizes (5 mm TL size-classes) on a plastic slate (Macpherson, 1998). Censuses were performed at the two studied spatial scales, focusing on the two studied seascape features: the microhabitat types (associated with a small boulder) and the wider meadow portions. First, we censed juveniles in microhabitats within the heterogeneous portions of the meadows in 2011 and 2012. At each site, for each microhabitat type, 10 random replicates of 25 cm x 25 cm point-count UVC (Cheminée et al., 2013; Francour and Le Direac'h, 1994; García-Rubies and Macpherson, 1995) were carried out. At each point-count, the trained diver visualized an imaginary plot were abundances and TL of juvenile fishes were recorded during 5 minutes. This size and this duration were suitable to record the interaction occurring at this spatial scale. Secondly, to take into account seascape features at a wider spatial scale, in 2013, juveniles were censed at twelve random replicate belt-transects of 6 m x 3 m within heterogeneous and within homogenous portions.

Furthermore, for subsequent analyses, due to the difficulty to identify underwater the species of juvenile fish, we decided to pool them by taxonomical groups that can be visually recognized and have similar ecological requirements (Harmelin, 1987; Lejeune, 1984). Crypto-benthic fish (including different taxa belonging to Blenniidae, Gobiidae and Tripterygiidae), due to their apparent low densities, were pooled as a single group. Other groups were as follows: *Symphodus* spp. (including *S. roissali*, *S. tinca* and *S. ocellatus*); *Serranus* spp. (including S. *cabrilla* and *S. scriba*); *Mullus* spp. *(M. barbatus* and *M. surmuletus*); *Pagellus* spp.; and Mugilidae. Afterwards, in order to refer to such groups we denominate them as "taxa". Taxa accounting in this study for more than 10% of the juvenile abundance were considered as "dominant". All other species or taxa were considered "minority" species.

II.2.4. Statistical analyses

At seascape scale, first, we used PERMutational multivariate Analysis Of Variance (PERMANOVA) to assess the differences of habitat descriptors (cover and height) between meadows structure types, sampling month and site. PERMANOVA model included 3 factors: i) "meadow structure" was fixed and included two levels (homogeneous and heterogeneous); ii) "sampling month" was also fixed and included 2

levels (July and September); and iii) "site", was random and included 3 levels (S1, S2 and S3). In order to illustrate the PERMANOVA results, a non-metric multi-dimensional scaling (nMDS) biplot of samples was employed (Clarke and Gorley, 2006). We used arrows superimposed to nMDS biplots to represent the Spearman rank correlations between biplot axes and meadow characteristics (Clarke and Warwick, 2001). For this analysis and representation, multivariate descriptors of meadow structure were previously standardized and Euclidean distance was used as measure of dissimilarity, due to the different nature and ranges of variation of the two descriptors used (cover and height) (Anderson and Gorley, 2008).

At seascape scale, secondly, we assessed the effect of meadow structure types, sampling months and site on juvenile assemblage's descriptors (univariate total density and richness, and the multivariate assemblage structure, i.e., comparative densities of each taxa), by means of PERMANOVAs with the same model as previously described. In order to represent dissimilarities between the juvenile assemblages, we employed a Principal coordinate analysis (PCO) ordinations plot of centroids of fish juvenile assemblage samples of the dummy factor combining the factors meadow structure, sampling month and sites (Clarke and Gorley, 2006). We used arrows superimposed to PCO biplots for representing the spearman rank correlations between biplot axes and taxa-specific densities (Clarke and Warwick, 2001). Euclidean distance was used as measure of dissimilarity for univariate response variables (total density and richness), and modified-Gower (base 2) was employed as measure of dissimilarity for multivariate juvenile assemblage structure. Indeed, it was well adapted to our data (see results) since this dissimilarity measure has the double advantage to both reduce heterogeneity of variance and down-weight the most abundant species without altering the data with any prior transformation (Anderson and Gorley, 2008).

At seascape scale, thirdly we assessed the effect of meadow structure, sampling month and site on taxa specific univariate descriptors, using univariate PERMANOVAs with the same model as previously.

Finally, at a lower, microhabitat scale, we tested if, on one hand, juvenile assemblage's descriptors (univariate total density and richness, and the multivariate assemblage structure (comparative densities of each taxa)), and on the other hand, dominant taxa specific univariate densities, varied between: i) microhabitat types; ii) sampling month;

iii) sampling years and iv) sites, by means of PERMANOVAs. PERMANOVA models included 4 factors: i) “microhabitat type”, fixed and with 3 levels (cy, sh and cn); ii) “sampling month”, fixed with 2 levels (July and September); iii) “sampling year”, random with 2 levels (2011 and 2012); and iv) “site”, random with 3 levels (S1, S2 and S3).

Sums of squares (SS) for these PERMANOVA designs were performed as a fully partial analysis (type III). P-values were obtained by 999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<200). Terms were pooled as suggested by Anderson et al. (Anderson and Gorley, 2008). Due to the intrinsic variability of ecological data, tests were considered significant for p-values <0.1.

Multivariate exploratory analyses and multivariate and univariate inferential tests were performed using the PRIMER 6 and PERMANOVA + B20 package (Anderson and Gorley, 2008; Clarke and Gorley, 2006). Data set manipulations and others graphical visualizations (univariate visualizations) were performed in R Environment (R Development Core Team, 2013) using the library ggplot2 (Wickham, 2009).

II.3. RESULTS

II.3.1. Effect of meadow structure type and sampling month on meadow descriptors

The nMDS plot revealed the trivial segregation between samples of different meadow structure (heterogeneous *versus* homogenous), because of differences in boulders presence and *Cystoseira* and shrubby algae cover (see PERMANOVA Table II-2, Table II-1 and Fig. II-3).

Table II-1.Recorded *Cymodocea nodosa* meadow characteristics in 2013 (mean ±se). Mean cover (%) and height (cm) of the components within each defined meadow structure types (homogeneous and heterogeneous) and according to sampling months (July and September) at 2013. Cover: covbo= boulders, covcn= *Cymodocea nodosa*; covcp= *Caulerpa prolifera*; covcy= *Cystoseira* spp.; and covsh= shrubby algae. Height: htbo=boulders, htcn= *Cymodocea nodosa*; htcp= *Caulerpa prolifera*; htcy= *Cystoseira* spp.; and htsh= shrubby algae.

		Homogeneous		Heterogeneous	
		July	September	July	September
Elements cover	Covbo	0.00±0.00	0.00±0.00	30.57±1.92	36.00±1.48
	Covcn	57.06±2.74	51.83±3.46	45.76±2.35	29.86±2.25
	covcp	12.14±2.07	15.72±2.17	6.51±1.34	11.50±1.39
	covcy	0.36±0.29	1.69±0.62	11.38±1.13	19.95±1.38
	covsh	0.00±0.00	0.06±0.06	18.73±1.92	17.22±1.47
Elements height	htbo	20-30	20-30	20-30	20-30
	htcn	18.69±0.76	15.83±0.59	18.78±0.96	14.19±0.56
	htcp	7.06±0.93	8.83±0.68	6.54±0.90	8.56±0.57
	htcy	1.03±0.72	3.72±1.10	13.62±1.12	11.83±1.03
	htsh	0.00±0.00	0.08±0.08	2.92±0.53	2.31±0.45

Additionally, a significantly higher cover and height of the green macroalgae *Caulerpa prolifera* and a lower cover of *C. nodosa* were recorded in the samples from the innermost sites of the bay (S2 and S3). Furthermore, macrophyte structure varied according to sampling month in every site and meadow structure type, with the higher *C. nodosa* cover observed in July (see PERMANOVA Table II-2, Table II-1 and Fig. II-3).

Table II-2. PERMANOVA table of results: effect of *Cymodocea nodosa* meadow structure type and sampling month on habitat descriptors.Significance=. P≤0.1 ; * P ≤ 0.05 ; ** P ≤ 0.01 ; *** P ≤ 0.001.

Source of variation	Df	MS	Pseudo-F	P(perm)
Meadow structure (me)	1	$3.69 \cdot 10^{-5}$	10.26	0.007**
Sampling month (sm)	1	25619	1.74	0.174
Site (si)	2	$1.10 \cdot 10^{-5}$	62.59	0.001***
mexsm	1	9163.1	2.41	0.149
mexsi	2	35976	20.54	0.001***
smxsi	2	14728	8.41	0.001***
mexsmxsi	2	3802.1	2.17	0.01*
Res	133	1751.3		
Total	144			

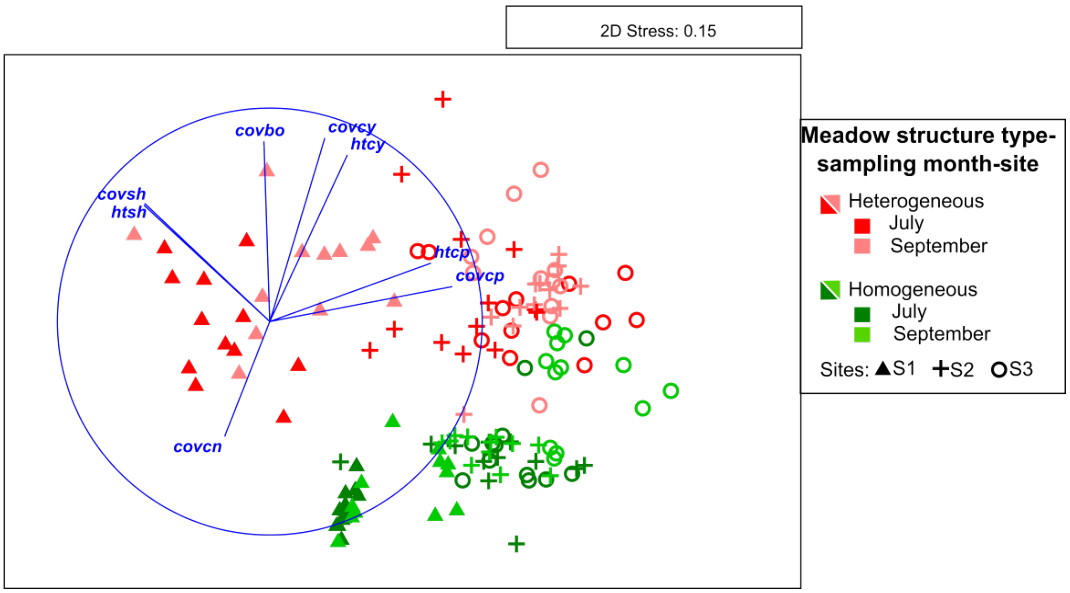

Fig. II-3. nMDS ordination plot of macrophyte descriptors of the *Cymodocea nodosa* meadows, according to defined meadow structure types (heterogeneous and homogeneous), sampling months (July and September) and sites (S1, S2 and S3). Correlation vectors (Spearman) of macrophyte cover and height (only correlations >0.4 are represented). Boulder cover: covbou; Macrophyte cover: covcn= *Cymodocea nodosa*; covcp= *Caulerpa prolifera*; covcy= *Cystoseira* spp.; covsh= Shrubby algae. Macrophyte height: htcn= *Cymodocea nodosa*; htcp= *Caulerpa prolifera*; htcy= *Cystoseira* spp.; htsh= Shrubby algae.

II.3.2. Effect of meadow structure type and sampling month on juvenile fish assemblage and taxa-specific trends

II.3.2.1. Total density and species richness

Total density and richness significantly differed between meadow structure types in both sampling months. Heterogeneous portions of the meadow had a higher total density and richness than homogeneous ones whatever the site. Additionally, the outermost site (S1) of the bay had always a higher species richness and juvenile density than the two innermost sites of the bay. Conversely, sampling month did not have any clear effect on total density pattern or species richness, although the interaction term meadow structure x sampling month x site was significant for total density (PERMANOVAs Table II-3, Fig. II-4).

Table II-3. PERMANOVA table of results: effect of *Cymodocea nodosa* meadow structure and sampling month on univariate descriptors of juvenile fish assemblage (total density and richness) and multivariate juvenile assemblage structure. Significance=· $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Response variable: total density				
Source of variation	**Df**	**MS**	**Pseudo-F**	**P(perm)**
Meadow structure (me)	1	60.47	83.21	**0.015***
Sampling month (sm)	1	3.97	2.05	0.271
Site (si)	2	21.30	16.00	**0.001*****
me x sm	1	0.57	$9.36 \cdot 10^{-2}$	0.785
me x si	2	0.73	0.55	0.558
sm x si	2	1.94	1.46	0.228
me x sm x si	2	6.14	4.61	**0.015***
Res	132	1.33		
Total	143			
Response variable: richness				
Source of variation	**Df**	**MS**	**Pseudo-F**	**P(perm)**
Meadow structure (me)	1	90.25	14.25	**0.073·**
Sampling month (sm)	1	8.03	1.47	0.345
Site (si)	2	83.53	51.32	**0.001*****
mexsm	1	7.11	1.92	0.320
mexsi	2	6.33	3.89	**0.021***
smxsi	2	5.44	3.35	**0.04***
mexsmxsi	2	3.69	2.27	0.118
Res	132	1.63		
Total	143			
Response variable: assemblage structure				
Source of variation	**Df**	**MS**	**Pseudo-F**	**P(perm)**
Meadow structure (me)	1	19.37	3.80	**0.064·**
Sampling month (sm)	1	19.61	3.14	**0.084·**
Site (si)	2	3.58	2.20	0.039*
mexsm	1	6.44	1.45	0.328
mexsi	2	5.09	3.13	**0.006****
smxsi	2	6.25	3.84	**0.001*****
mexsmxsi	2	4.45	2.73	**0.009***
Res	132	1.63		
Total	143			

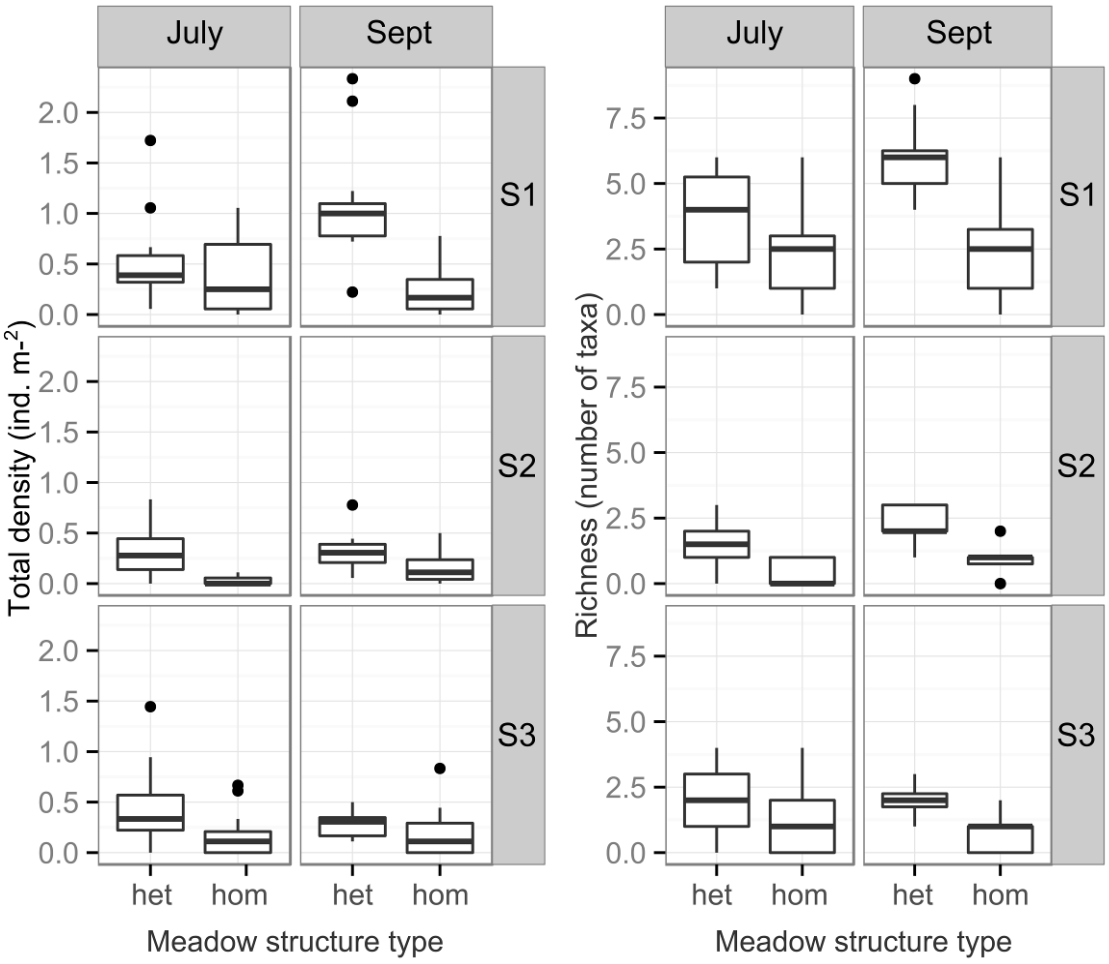

Fig. II-4. Boxplots of total fish density and richness within sampled sites (S1, S2, S3) according to *Cymodocea nodosa* meadow structure types (heterogeneous and homogeneous) and sampling months (July and September). Box plots indicate the median (bold line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the inter quartile range (whiskers), and remaining outliers (open circles).

II.3.2.2. Differences in assemblage structure and taxa-specific trends

In 2013, the juvenile assemblage structure significantly differed between meadow structure types and sampling months (see PERMANOVAs, Table II-3 and Fig. II-5). On one hand this reflected the taxa composition differences in both meadow structure types, and a higher taxa number (i.e. richness described above) in heterogeneous portions of the meadow: *C. julis* and *Serranus* spp. were observed only in heterogeneous portions of the meadow while *L. mormyrus*, *S. viridensis* and *Pagellus* spp. (a single individual) were only observed in homogeneous portions of the meadow (Table II-4). On the other hand this assemblage difference also reflected the higher density in heterogeneous

portions of the meadow of most of the species shared by both meadow structure types (Table II-4). Finally it also reflected sampling month trends for some species. More particularly, among the dominant taxa, *D. annularis* displayed similar densities in heterogeneous and homogeneous portions of the meadow and was more abundant in September than in July in the three sites. *Symphodus* spp. density also peaked in September, but they were more abundant in heterogeneous portions than in homogeneous ones in 4 of the 6 combination of season x site. Furthermore, although low frequency of *S. salpa* did not allow conclusive tests, it tended to be more abundant in July *versus* September and in heterogeneous portions of the meadow *versus* homogeneous ones (see PERMANOVAs, Table II-5, Table II-4 and Fig. II-6).

Table II-4. Juvenile fishes observed in the *Cymodocea* meadows in 2013 : number of juvenile fish in heterogeneous portions of the meadows (n het), number of juvenile fish in homogenous portions (n hom), number of juvenile fish in July (n july), number of juvenile fish in September (n sept), number of juvenile fish in sites (n S1, n S2, n S3), total number of juvenile censed (n tot), dominance categories, mean TL (mm ± se), minimum (Min) and maximum (Max) TL (mm). Total sampled area = 2592 m².

Species	n het	n hom	n july	n sept	n S1	n S2	n S3	n tot	Dominance	Mean (TL ± se)	Min TL	Max TL
Coris julis	27	0	14	13	27	0	0	27	minority	49.67±3.18	15	60
Dicentrarchus labrax	7	2	9	0	0	5	4	9	minority	68.00±10.20	40	90
Diplodus annularis	109	71	42	138	76	27	77	180	dominant	45.60±1.20	10	70
Diplodus sargus	49	35	35	49	38	33	13	84	minority	58.09±2.51	25	90
Diplodus vulgaris	41	27	33	35	40	14	14	68	minority	56.80±2.32	20	90
Lithognatus mormyrus	0	2	2	0	0	2	0	2	minority	77.50±12.50	65	90
Mugiilidae	7	5	7	5	0	0	12	12	minority	51.67±7.26	40	65
Mullus spp.	18	9	18	9	26	1	0	27	minority	76.00±4.76	40	90
Oblada melanura	48	10	0	58	58	0	0	58	minority	48.82±2.37	30	60
Pagellus spp.	0	1	1	0	1	0	0	1	minority	50	50	50
Pagrus	2	2	4	0	0	1	3	4	minority	78.33±21.67	35	100
Sarpa salpa	132	69	192	9	56	43	102	201	dominant	50.00±2.91	15	100
Serranus spp.	6	0	2	4	5	1	0	6	minority	71.67±4.01	60	80
Sphyraena viridensis	0	6	6	0	6	0	0	6	minority	70	70	70
Spondyliosoma cantharus	5	2	7	0	7	0	0	7	minority	52.50±10.31	30	70
Symphodus spp.	187	19	34	172	148	45	13	206	dominant	49.58±1.31	15	65
Sparus aurata	5	5	4	6	7	0	3	10	minority	87.86±8.85	45	120
Blenniidae-Gobiidae-Tripterygiidae	1	0	1	0	0	0	1	1	minority	45	45	45

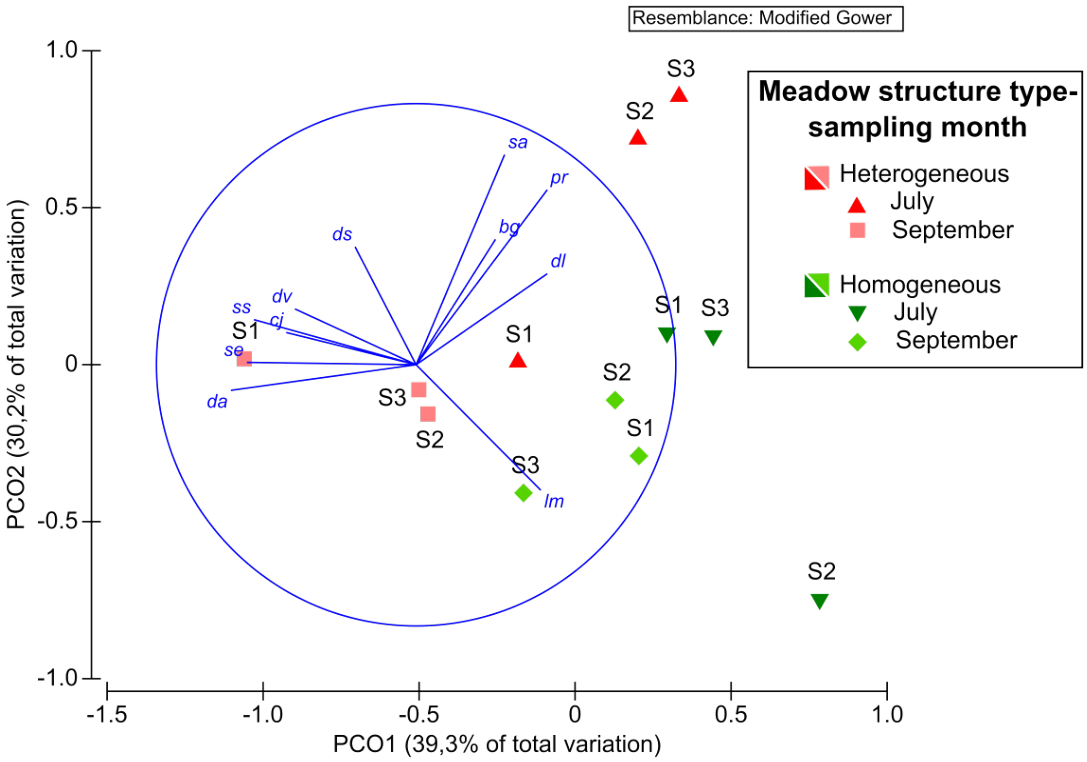

Fig. II-5. Principal coordinate analysis (PCO) ordinations plot of centroids of fish juvenile assemblage samples within *Cymodocea nodosa* meadows according to meadow structure types (heterogeneous and homogeneous), sampling months (July and September) and sites (S1, S2, S3). Correlation vectors (Spearman) of taxa specific densities (in blue) are plotted (for correlations >0.4). Taxa: bg=Blenniidae-Gobiidae-Tripterygiidae; da=*Diplodus annularis*; dl=*Dicentrarchus labrax*; ds=*Diplodus sargus;* dv=*Diplodus vulgaris;* cj=*Coris julis;* lm=*Lithognathus mormyrus;* mu=*Mullus* spp.*;* om=*Oblada melanura;* pr=*Pagrus pagrus;* sa=*Sarpa salpa;* se=*Serranus* spp.; ss=*Symphodus* spp.

Table II-5. PERMANOVA table of results: effect of *Cymodocea nodosa* meadow structure type and sampling month on univariate taxa-specific densities of juvenile dominant species. Significance=· $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Response variable: *D. annularis* density				
Source of variation	**Df**	**MS**	**Pseudo-F**	**P(perm)**
Meadow structure (me)	1	$3.05 \cdot 10^{-2}$	3.18	0.239
Sampling month (sm)	1	0.20	5.71	0.162
Site (si)	2	$5.40 \cdot 10^{-2}$	5.62	**0.004****
mexsm	1	$2.55 \cdot 10^{-2}$	2.14	0.251
mexsi	2	$9.61 \cdot 10^{-3}$	1.00	0.371
smxsi	2	$3.51 \cdot 10^{-2}$	3.65	**0.032***
mexsmxsi	2	$1.20 \cdot 10^{-2}$	1.24	0.304
Res	133	$9.61 \cdot 10^{-3}$		
Total	144			
Response variable: *S. salpa* density				
Source of variation	**Df**	**MS**	**Pseudo-F**	**P(perm)**
Meadow structure (me)	1	$7.69 \cdot 10^{-2}$	0.54	0.533
Sampling month (sm)	1	0.70	21.40	0.048
Site (si)	2	$6.76 \cdot 10^{-2}$	2.50	**0.069·**
mexsm	1	$5.33 \cdot 10^{-2}$	0.43	0.62
mexsi	2	0.14	5.32	**0.006****
smxsi	2	$3.25 \cdot 10^{-2}$	1.21	0.304
mexsmxsi	2	0.12	4.59	**0.007****
Res	133	$2.70 \cdot 10^{-2}$		
Total	144			
Response variable: *Symphodus* spp. density				
Source of variation	**Df**	**MS**	**Pseudo-F**	**P(perm)**
Meadow structure (me)	1	0.61	3.57	0.174
Sampling month (sm)	1	0.41	3.60	0.193
Site (si)	2	0.32	22.29	**0.001*****
mexsm	1	0.33	4.85	0.161
mexsi	2	0.17	11.82	**0.001*****
smxsi	2	0.11	7.96	**0.002****
mexsmxsi	2	$6.88 \cdot 10^{-2}$	4.78	**0.004****
Res	133	$1.44 \cdot 10^{-2}$		
Total	144			

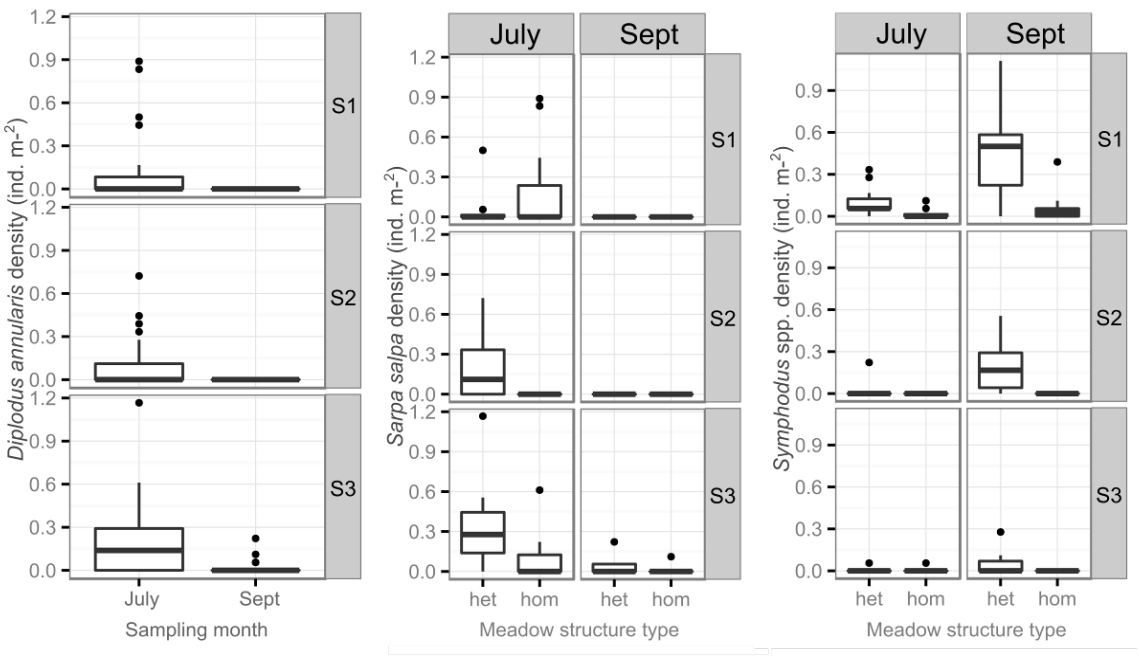

Fig. II-6. Boxplot of *Diplodus annularis*, *Sarpa salpa* and *Symphodus* spp. densities in *Cymodocea nodosa* meadows according to significant terms (see PERMANOVA Table II-5). Meadow structure types: het: heterogeneous, hom: homogeneous; sampling months: July, Sept: September; sites: S1, S2, S3. See Fig. II-4 for explanation of box plots elements.

II.3.3. Effect of microhabitats on juvenile assemblage and taxa-specific trends

A total of 14 taxa of juveniles fishes were observed in the three microhabitats types within the heterogeneous portions of the meadow in 2011 and 2012 (Table II-6).

Table II-6. Juvenile fishes observed in the three microhabitats within heterogeneous portions of *Cymodocea nodosa* meadows in 2011 and 2012. Total number (n), dominance categories, mean TL (mm ± se), minimum (Min) and maximum (Max) TL (mm). Total sampled area = 330 m².

	2011					2012				
Species	Dominance	n	Mean (TL ± se)	Min TL	Max TL	Dominance	n	Mean (TL ± se)	Min TL	Max TL
Dentex dentex	minority	3	76.67±14.53	50	100	not recorded	0	-	-	-
Diplodus annularis	minority	8	51.25±6.93	10	70	dominant	102	42.25±1.44	15	75
Diplodus sargus	minority	43	56.86±1.97	35	90	dominant	171	51.26±1.33	20	90
Diplodus puntazzo	minority	4	87.50±7.50	70	100	minority	7	67.14±5.33	45	80
Diplodus vulgaris	minority	43	65.23±2.16	40	90	minority	21	54.05±2.88	30	80
Mullus spp.	minority	1	30	30	30	minority	1	80	80	80
Oblada melanura	minority	11	46.36±4.91	30	90	minority	9	53.33±4.86	25	70
Pagellus spp.	minority	2	95.00±5.00	90	100	minority	1	50	50	50
Sarpa salpa	dominant	72	54.03±1.25	30	80	minority	40	54.50±3.26	25	100
Serranus spp.	minority	3	83.33±3.33	80	90	minority	7	60.00±6.07	40	80
Sphyraena viridensis	not recorded	0	-	-	-	minority	1	70	70	70
Spondyliosoma cantharus	not recorded	0	-	-	-	minority	4	82.50±18.87	50	120
Symphodus spp.	dominant	58	41.90±1.45	15	65	dominant	73	43.42±1.12	20	65
Blenniidae-Gobiidae-Tripterygiidae	minority	5	35.00±2.24	30	40	minority	7	40.00±1.54	35	45

Total density, richness, assemblage structure or density of dominant taxa (*D. annularis*, *D. sargus*, *S. salpa* and *Symphodus* spp.) did not differ between microhabitats types or sampling months (PERMANOVAs, all $p>0.1$).

II.4. DISCUSSION

The presence of boulders within the seagrass meadow resulted into a higher density of juvenile fishes and a higher species richness at a scale of tens of meters but not at a lower scales, as no differences existed among microhabitats. This is probably because the home range of juvenile fishes was larger than the size of the microhabitats (25 cm x 25 cm) but lower than that of the transects (6 m x 3 m). Furthermore, position within the bay may have had an effect on species richness and density, as both increased closer to

the mouth, although some species like *S. sarpa* and *D. annularis*, strongly associated to seagrass meadows, were more abundant at the innermost sites.

The structure of the *C. nodosa* meadows at Fornells bay varied also between the outermost and the innermost sites, primarily because the cover of *C. prolifera* increased and that of *C. nodosa* decreased at the innermost sites (Delgado et al., 1997; Fàbregas, 2007; this study). Competitive interactions between *C. prolifera* and *C. nodosa* have been reported in other studies (Pérez-Ruzafa et al., 2012; Tuya et al., 2013) and the final outcome is probably related to confinement. This pattern may respond to the strong and frequent north winds which determine the hydrodynamics of the bay, as evidenced by the sediment distribution (Fornos et al., 1992) leading to more sediment re-suspension in the inner (south) parts of the bay, decreasing light levels, and affecting the growth of the *C. nodosa* (Marba and Duarte, 1994). Furthermore, another plausible explanation is the low renewal of water in the inner parts of the bay, since water flow may play an important role for *C. nodosa* seagrass performance and survival in areas with low dissolved oxygen conditions (Binzer et al., 2005).

Nevertheless, it is unlikely that the changes observed in the fish assemblage between sites are related to the relative cover of *C. prolifera* and *C. nodosa*. Site S1 was in the vicinity of the wide strait communicating the bay with the open sea, which may lead to higher supply of eggs and larvae, even more when taking into account that frequent north winds determine the hydrodynamics of the bay. In this sense, many authors suggested the importance of the position of the habitat in enclosed coastlines (Bell et al., 1988; D'Alessandro et al., 2007; Jenkins et al., 1998; Martins et al., 2007) ; and the location of a seagrass bed within an enclosed landscape has been highlighted to have a more significant effect on abundances of juveniles of many species of fish and decapods, than the size, shape, leaf height or leaf density of the seagrass meadow (Bell et al., 1988).

Independently on the location within the bay, fish assemblages varied between homogenous *versus* heterogeneous portions of the meadows, with higher densities and species richness of juvenile fish in heterogeneous portions. In this sense, our results support the importance of meadows structure at the scale of tens of meters in determining assemblage structure of juveniles. Dahlgreen and Eggleston (2000) state that the best juvenile habitat provides a trade-off between food availability and shelter

against predation, i.e. a high habitat quality. We can hypothesise that juvenile fishes inhabiting heterogeneous meadow portions may benefit from more diversified food and/or shelter resources (more ecological niches), provided by the different microhabitat types through their complementarities and/or synergy , i.e., edge effects (Dorenbosch et al., 2005; Horinouchi, 2007). Indeed, the small open spots provided in the meadow by boulders generate small ecotones, i.e., edges within the seagrass meadow (Kolasa and Zalewski, 1995). At the ecotones, organisms may regularly switch between habitats and therefore exploit alternatively the optimum micro-habitat as regards to the resource expected (food or shelter) (Cheminée, 2012). Edges may provide more food for omnivorous juveniles due to the greatest abundance of crustacean or other invertebrates at the seagrass boundaries (Macreadie et al., 2009; Tanner, 2005; Warry et al., 2009). Additionally, predation has been reported to be less effective in the edges (Hovel and Lipcius, 2001; Smith et al., 2011) (but see other studies (Thiriet, 2014)) In this sense, juveniles can forage efficiently in the risky habitat and switch when a predator is detected. Edge effect has been reported to influence density of fish in other studies (Jelbart et al., 2006; Macreadie et al., 2009; Smith et al., 2010).

However, more structured meadows may not necessarily favor all the fish species. *Symphodus* spp. and *S. salpa* densities increased in more structured sectors in the meadows, whereas the density of *D. annularis* was similar in the two types of sectors in the meadow. These observations are in agreement with those of previous studies which reported that inside the meadow some species have adapted life-strategies (anti-predator and foraging tactics) for more structured seagrass meadows, whereas others may be adapted to sparser seagrasses or opened areas adjacent to its edge, or others even do not respond to changes in complexity in the seagrass (Horinouchi, 2007; Orth et al., 1984).

Symphodus spp. juveniles are necto-benthic fish highly sedentary, with quite a small home range (Harmelin, 1987) and usually are associated with complex habitats (Cheminée, 2012) (see also Chapter III). They have a typical morphology of manoeuvrable epibenthic foragers. Juveniles of some species of this genus (e.g. *S. ocellatus*) have been reported to eat mostly planktonic, epibenthic and bentic meiofauna (e.g. copepods) commonly present near or on the boulder substratum (Levi, 2004). In this sense they can profit the resources upon the boulders. Furthermore, *Symphodus* spp. juveniles (and Labrids in general) do not have a morphology of fast

speed swimmers (Hoar and Randall, 1979; Keast and Deirdre, 2011; Leis et al., 2011; Motta et al., 1995; Recasens et al., 2006); they are pale brown, which provide them a great camouflage and display cryptic behaviours hiding in the algae canopy (see Chapter III). In this sense, their anti-predator tactics are largely dependent on habitat structure. Such color patterns may be functional to camouflage in the seagrass or in the *Cystoseira* spp. upon the boulders. Furthermore it is plausible that they use holes, crevices and borders of small boulders to shelter. The presence of boulders in the meadow may favor both their foraging efficiency and safety.

On the other hand, both *S. salpa* and *D. annularis* are better swimmers and are considered necto-benthic fish with medium lateral and vertical movements (Harmelin, 1987; Jadot et al., 2006). *S. salpa* is silvery with yellow golden bands, and *D. annularis* is initially yellow and becomes silvery as grows up. Such colour patterns may favoured their camouflage in the seagrass meadows, were sun generate golden reflexion in the water; in this sense such species would not depend on boulders to shelter. Indeed, silver-yellow colour patterns of fish has been often highlighted to strikingly match to backgrounds and bodies of horizontally viewed water providing the camouflage of species (Donnelly and Dill, 1984; Marshall, 2000; Marshall et al., 2003). Moreover, *S. salpa* juveniles feed seaweed fragments and photophilous epilithic algae, such as *Halopteris,* whereas they feed seagrass leaf when they are sub-adults or adults (Havelange et al., 1997; Verlaque, 1990). Contrarily, *D. annularis* juveniles are omnivorous but the most important component reported in their diet is Chlorophyte algae (Matić-Skoko et al., 2004). In the *C. nodosa* meadow at Fornells bay, *C. prolifera* is the most extensive Chlorophyte and it extends similarly in the two defined structural sectors within the meadow, whereas boulders epilithic algae belonged mainly to Dictyotales and Sphacelariales. In this sense, *S. salpa* may have had a trophic attachment with the boulders, whereas *D. annularis* may not.

Although fish assemblages varied between homogeneous and heterogeneous portions of the meadows, they did not vary at a smaller spatial scale within heterogeneous portions of the meadows. These results suggest that the composition of the juvenile assemblage is related to seagrass meadow structure but that the factors structuring juveniles assemblages are scale-dependent, operating at intermediate spatial scale of tens of meters, but not at lower scales of less than 1 meter. Anderson and Millar (2004)

reported high variability between lower spatial scales, e.g between transects 5 m apart due to the larger scale mobility of fish. So, the non-significant effects of the three microhabitat types may suggest that habitat structure do not operate at such scales to determine fish juvenile densities, since mobility of fish is larger. We hypothesize that it is the emergent overall three-dimensional structure which resulted from the aggregation of various structures among the meadow (microhabitats) which influenced juvenile assemblages, resulting in different and richer assemblages of juveniles in heterogeneous portions *vs* homogeneous portions. In this sense, the influence of habitat structure should be studied at adequate scales according to the studied organisms.

Finally, season might explain some variations between sampling months. The changes observed in juvenile assemblages between sampling months may respond primarily to the known settlement temporality of these species rather than to seasonal changes in seagrass structure, although meadow complexity decreased in September, when the cover of *C. nodosa* declined as a result of decreasing water temperature (Marba et al., 1996). For instance, the density of *Symphodus* spp. were higher in September than in July, because *S. roissali* and *S. tinca* reproduce first in April and then start to settle in June-July while *S. ocellatus* reproduces in June and settles in August-September and usually in much higher densities (Lejeune, 1985 ; Garcia-Rubies and Macpherson, 1995; Cheminée et al., 2013). *D. annularis* settles from June to September in the NW Mediterranean, which may explain why higher densities were recorded in September, when the settlement period comes to the end (Bussotti and Guidetti, 2010; Harmelin-Vivien et al., 1995). Finally, *S. salpa* was more abundant in July than in September, which is logical since its first settlement pulse usually occurs early in May-June (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995).

In summary, in agreement with the habitat quality trade off hypothesis, our results support a spatial partitioning of resources, which have been also highlighted in others habitats (Harmelin-Vivien et al., 1995) (see as well Chapter III).

II.5. CONCLUSIONS

As a conclusion, variations of meadow structure and seasons had additive effects explaining changes in fish juvenile assemblages in *C. nodosa* meadows at Fornells Bay. However, the influence of meadow structure was scale-dependent: structurally different microhabitats inside the meadow did not conduce to differences in juvenile fish density distributions, but more structured portions of the meadow with small boulders determined variations of fish assemblages, leading to richer ones. So, we can conclude that it is the emergent overall three-dimensional structure, resulting from the aggregation of the patches, which influenced juvenile distributions. However, not all species were positively influenced by the more structured sectors. We argue that the optimum production of juveniles of different species in such seascapes is acquired through the intrinsic structural variability of seagrass seascapes, displaying a mosaic of various habitat characteristics, and therefore fulfilling the contrasted needs of different species.

Chapter III. Effect of depth and *Cystoseira* forest three-dimensional structure on juvenile fish distribution patterns and behaviors

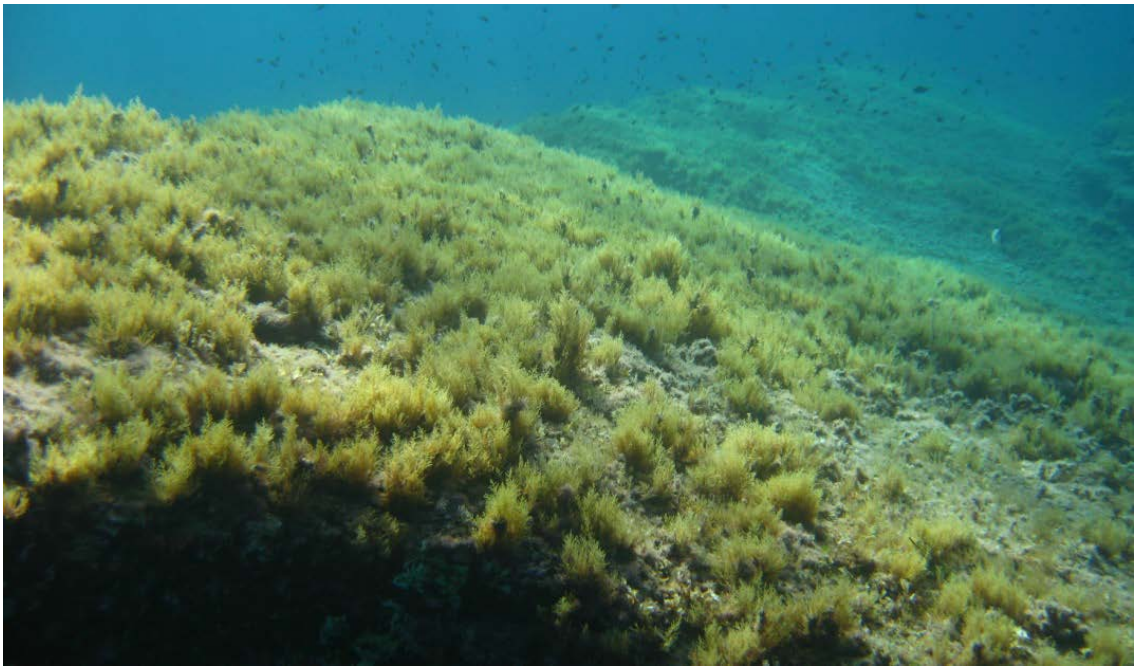

Photo III-1. *Cystoseira brachycarpa* var. *balearica* forests in Minorca island, depth = 8 meters, October 2013. Foreground spans around 3 m wide. Photo: Eva Vidal.

This chapter will be adapted and submitted in 2015 to an international journal (Marine Ecology Progress Series – 5YIF 3.1), with the co-authors as follow:

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Chapter III. Effect of depth and *Cystoseira* forest three-dimensional structure on juvenile fish distribution patterns and behaviors

III.1. INTRODUCTION

III.1.1. Context of this study

Chapter II showed how the three-dimensional structure of *Cymodocea nodosa* meadows, at various spatial scales, can influence juvenile fish assemblages. Here in Chapter III, we focused on the study of another infralittoral habitat important for juvenile fishes: the *Cystoseira* (Phaeophyceae) forests covering subtidal rocky bottoms.

The Mediterranean basin is considered as a hot-spot of diversity for *Cystoseira* species (Gianni et al., 2013). They are important foundation species in the Mediterranean euphotic zone (Feldmann, 1937; Giaccone, 1973) and are very productive, holding a high phytal and invertebrates biodiversity (Ballesteros, 1990a, 1990b, 1988; Pitacco et al., 2014), as well constituting a preferential habitat for the different life cycle stages of many common coastal fish (Cheminée et al., 2013; Lejeune, 1984; Rodrigues, 2010; Thiriet, 2014). However, conspicuous historical declines of subtidal *Cystoseira* forests have been reported in many regions (Airoldi and Beck, 2007; Gianni et al., 2013; Thibaut et al., 2014, 2005). Different European initiatives emphasise the urgency of their protection. For example, five species are listed in Annex I of the Bern Convention, and the whole genus (except *Cystoseira compressa*) is included in The Action Plan for the Conservation of Marine Vegetation in the Mediterranean Sea, adopted within the framework of the Barcelona Convention, which identifies the conservation of *Cystoseira* forests as a priority. However, *Cystoseira* forests remain poorly considered in the European Habitats Directive.

Cystoseira forests have been suggested to display a high nursery value (i.e. production of juveniles per unit of surface, *sensu* Beck et al. (2001)) for some Labridae and

Serranidae fish species (Cheminée et al., 2013). This is because *Cystoseira* forests present higher densities of such species than less structured habitats such as shrubby assemblages dominated by Dictyotales and Sphacelariales across large spatial scales of hundreds or thousands of kilometres (Thiriet, 2014). Habitat structure is defined as the amount, composition and three-dimensional arrangement of physical matters (both abiotic and biotic) at a location. It is composed by complexity (absolute abundance of individual structural components) and heterogeneity (relative abundance of different structural components) under a determinate spatio-temporal scale (Beck, 2000; Bell et al., 1991; Byrne, 2007). In other habitats comparisons, habitat structure has been proved as well to exert a great influence on juvenile fish assemblages (Guidetti, 2000; Jenkins and Wheatley, 1998; Laegdsgaard and Johnson, 2001; Levin and Hay, 1996; Nagelkerken and Van der Velde, 2002); usually most structured habitats harboured richer and more abundant juvenile fish assemblages (but see e.g. Grenouillet et al. (2002) and Guidetti and Bussotti (2002)). These differences have been attributed to the higher availabilities of both prey and shelter for juveniles in the more structured habitats, reducing starvation-and/or predation-induced mortalities compared with other less structured habitats (e.g. (Thiriet, 2014)).

At scale of fish, for a given habitat, when considering the variables quantifying the structuration degree of a given structural component in the habitat, e.g. a given type of macrophytes, it has been sometimes used the verticality, i.e, the development of vertical strata (as a measure of complexity) and the patchiness or coverture (as a measure of heterogeneity) (August, 1983; García-Charton et al., 2004; Guidetti and Bussotti, 2002; Wilson et al., 2007). They both define the macrophyte three-dimensional structure. More structured versions of the same macrophyte meadow increase fish densities and sizes (Cheminée, 2012; Cheminée et al., 2013; Levin and Hay, 1996; Parsons et al., 2014), and also influence the behavior of fish (i.e. the type of relationship with the bottom) (Cheminée, 2012; Lejeune, 1985); for example more structured macrophytes favoured a more resident behavior. Furthermore, behavior of fish is size dependent: in structured macrophytes, smaller fish of a given species display more resident behavior *versus* larger ones (Cheminée, 2012). Consequently, habitat structure may explain the reported variability of juvenile density distributions within a *Cystoseira* forest (Cheminée, 2012).

However, understanding the spatial variability of fish density requires notably to disentangle the part of it due to habitat structure from the part explained by other factors of the environment (Anderson and Millar, 2004; Friedlander and Parrish, 1998; García-Charton et al., 2004; McCoy and Bell, 1991). In turn, since habitat structure is an important source of natural variability of fish density distributions, it interferes in the obtained conclusions when aiming to evaluate factors which contribute as well to the spatial variability of fishes for a given habitat, such as depth and protection level.

Indeed, both depth and protection has been reported to exert a great influence on juvenile density distributions. Depth influences juvenile assemblage composition since juvenile depth distributions are taxa-specific (Francour, 1997; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Vigliola and Harmelin-Vivien, 2001). For example, juvenile labrids concentrate in the shallowest 10 meters (García-Rubies and Macpherson, 1995; Letourneur et al., 2003). However, bibliography documenting fish juveniles depth distributions remains scarce in the Mediterranean. Furthermore, juvenile depth distributions are size-dependent in some cases, since for some species, the smallest juveniles present a narrower depth range distribution than larger ones (Vigliola, 1998). In marine organism, depth gradients are also characterized by significant differences in the intensity of trophic linkages. This may interact with any effects derived from other factors of interest, such as protection. For instance, Vergés et al (2012) found an increase in predation of sea urchins within MPAs but only in shallow waters, where their fish predators concentrate.

The establishment of well-enforced marine protected areas (MPA) usually allows the rebuilding of the natural adult biomass of exploited species (Edgar et al., 2014; García-Charton et al., 2008; Gaston et al., 2008; Halpern, 2003; Lester et al., 2009; Mora and Sale, 2011). This shapes the spatial distribution, including depth distribution, of adult predators and con-specifics of juveniles (Bell, 1983; Roberts and Polunin, 1993). Consequently, protection may indirectly shape juveniles spatial distributions within a given habitat, including depth distributions (Arceo et al., 2012; Hereu, 2004; Jones, 1987; Tupper and Boutilier, 1995; Tupper and Juanes, 1999). Indeed, it has been observed that protection increases mortality of juveniles, not targeted by fishing, inside MPAs due to the favoured presence of larger and more numerous predators (Gruss et al., 2011; López-Sanz et al., 2011; Tupper and Juanes, 1999) ; however this is not a

generalised process (Macpherson et al., 1997; Planes et al., 1999) and effects of protection is still unclear for the early phases of fish. For example, it has been suggested that only bigger juveniles (recruits) may suffer a higher predation mortality inside MPAs, because smaller juveniles (settlers) are predated by smaller predators, which are not targeted by fishing and are therefore present in similar densities inside or outside marine reserves (Planes et al., 1999). Furthermore, as regards to con-specifics adults, it has been reported some competitive interactions among adults and juveniles, where juveniles decrease their growth or increase their mortality due to competitive interactions with adults (Jones, 1987; Tupper and Boutilier, 1995). In this sense, MPAs, whit larger and more numerous adults may intensify these competitive interactions. More studies are needed to elucidate the effects of protection on juvenile fish, taking into account possible depth changes in the intensity of trophic linkages, which remain still unstudied.

In summary, previous studies (cited above) support that within-habitat variability in fish juvenile densities depends strongly upon habitat structure, depth and adult assemblages. However, little is known about the interactive or separated effects of habitat structure, depth and protection on juvenile fish distribution patterns within subtidal Mediterranean rocky reefs and more particularly within *Cystoseira* forests.

III.1.2. Objectives of Chapter III

In this context, the purpose of this chapter is to study the juvenile assemblage (in terms of total densities, richness and assemblage structure), and the taxa-specific trends (densities, sizes and behavior) within *Cystoseira* forests according to three possible drivers: i) forest structure (i.e. canopy height and cover); ii) depth (considering three depth strata between 0 and 12 meters) and iii) protection levels (comparing no-take *versus* non-protected areas). Our main hypothesis states that juvenile fish assemblage associated to *Cystoseira* forests and taxa-specific trends of juveniles dwelling into this habitat are significantly influenced by both *Cystoseira* site-specific three-dimensional structure and depth. Moreover, we hypothesized that depth-related trends, for both the whole juvenile assemblages and taxa-specific descriptors, may also be influenced by the protection level (i.e. inside *vs* outside marine reserve) due to possible different vertical distributions of adult predators and con-specifics. This knowledge is important in order to design future management actions that assure a supply of juveniles and therefore an adequate replenishment of adult fish populations.

III.2. MATERIAL AND METHODS

III.2.1. Studied area

The study was conducted in the northern coast of Minorca island (Balearic Archipelago) (Fig. III-1), where rocky bottoms and seagrass meadows prevail in the infralittoral, with a few areas of bare sand. Rocks made of magnesium carbonate alternate throughout the whole region with non-carbonated rocks, mainly shale and some basalts (Rosell and Llompart, 2002). Over rocky bottoms, extensive areas of *Cystoseira brachycarpa* J. Agardh, 1986 forests thrive from 1 to 15 meters depth (Sales and Ballesteros, 2009) (Photo III-1). The MPA "Reserva Marina del Nord de Menorca" was established in 1999 in the northern coast of Minorca (Fig. III-1). However, its enforcement and monitoring began only in 2000 (Coll et al., 2012). The MPA covers 5.20 km^2 and most of it can be classified as partial reserve, as some fishing is still allowed (Coll et al., 2012). Fishing has been totally banned in only two no-take areas, the first covering 838 ha of rocky bottoms in the west and the second one covering 217 ha of soft bottoms in the innermost part of Fornells bay (Coll et al., 2012). Fish biomass, including fish predators, increased steadily both in the no-take and the partial reserve areas after the establishment of the MPA and was close to carrying capacity in 2005 (Cardona et al., 2013, 2007b; Coll et al., 2012).

III.2.2. Sampling design

Sites were selected after a broad exploration of north coast looking for rocky bottoms covered by wide and dense *Cystoseira* forests, with a percentage cover higher than 50%, outside and inside the MPA and at the three depth strata considered in the study (i.e. d1: 3-5 m, d2: 6-8 m, d3: 10-12 m). In order to avoid possible confounding effects between our study variables and other environmental variables, the selected sites were similar in terms of rock surface (flat rock), slope (≥45º) and exposure (all locations were exposed to wave effects). Furthermore, selected *Cystoseira* bottoms were only intermingled with shrubby-turf algae (>2.5 cm).

Juvenile fish assemblages associated to *Cystoseira* forests were sampled in two consecutive years (2012 and 2013). In 2012 the study design aimed to test the putative

effects of depth and *Cystoseira* forest three-dimensional structure on juvenile fish assemblage (total densities, richness and assemblage structure) as well as on taxa specific descriptors (densities, sizes and behavior). In order to state the within forest variability in these putative effects (their general consistency), the design was composed by 2 nested spatial scales (Fig. III-1). At broad spatial scale (~10-30 km), 2 locations were sampled (B and C). At fine spatial scale (~500 meters), 3 sites were studied within each location (B: sites 2, 3 and 4; C: sites 5, 6 and 7). In 2013 we redistributed our sampling effort in order to additionally test for the effect of protection on juveniles and adults fish by using an 'After Control-Impact' approach (Underwood, 1997) (Fig. III-1). We sampled 3 protected sites (Impact) within the location B (NTZ) (the same sites than previous year) and we sampled 3 unprotected sites (Control) outside the MPA. Protected and Unprotected sampling sites were not spatially interspersed since there is only one NTZ protecting *Cystoseira* forests in Minorca. Nevertheless, we sampled unprotected sites on both sides of the NTZ (westward: site 1; eastward: sites 7 and 8) in order to minimize possible confounding effects between putative protection effects and 'location' effects (related to other natural environmental factors).

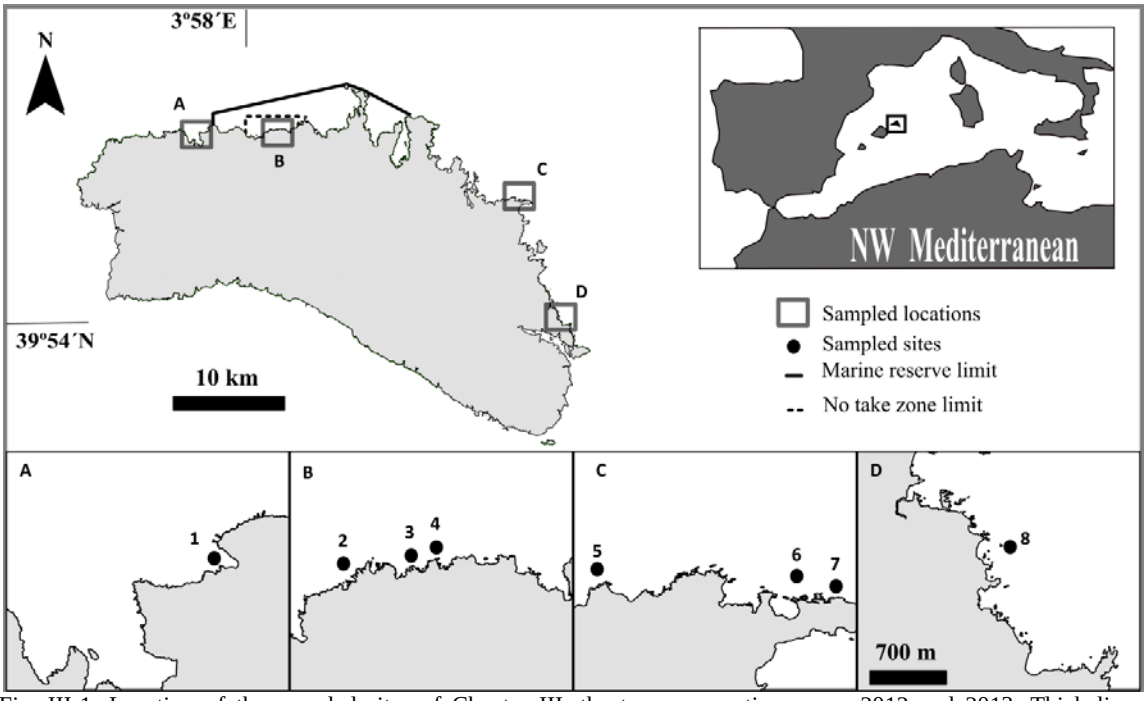

Fig. III-1. Location of the sampled sites of Chapter III, the two consecutive years: 2012 and 2013. Thick line represents MPA limits. Thick dotted line represents no-take zone limit. Empty squares are study locations. Sites (black dots) were: 1 (40° 3'26.64 N, 3° 59'27.36 E), 2 (40°03'593 N, 4°00'099 E), 3 (40°03'554 N, 3°59'956 E), 4 (39°59'956 N, 4°15'748 E), 5 (39°59'971 N, 4°15'553 E, 6 (40°00´71 N, 4°14´250 E), 7 (40º3´28.07" N, 3º55´41.82" E), and 8 (39º55´34.07" N, 4º17´23.02" E).

III.2.3. Data collection

Field surveys were conducted from September 23th to October 15th 2012 and from September 24th to October 15th 2013. This sampling period coincides with the presence within nursery habitats of juveniles of many Mediterranean littoral fish species, more particularly some labrid species such as *Symphodus ocellatus* and *Coris julis* (Froese and Pauly, 2011; García-Rubies and Macpherson, 1995; Lejeune, 1985, 1984; Raventos and Macpherson, 2001). This time of the year also coincide with the period when differences in fish densities (including predators) caused by recreational fishing are maximized (Cardona et al., 2007a) which may allow us to more easily detect differences between inside and outside reserve. Moderate and rough sea states as well as poor visibility days were avoided.

In order to sample juvenile fish assemblages and taxa-specific trends, during daylight (between 9 am and 4 pm), 8 random replicates of 1 m² point-count UVC (Cheminée et al., 2013; Francour and Le Direac'h, 1994; García-Rubies and Macpherson, 1995) (scattered over ~50 m²) were carried out in each depth strata of each site, by previously inter-calibrated SCUBA divers. At each point-count, the trained diver visualized an imaginary 1 m² plot where abundances, total length (TL) and behavior of fish were recorded, during 5 minutes. Such surface for a replicate, combined with the chosen duration, allowed us recording fish juvenile interactions with the habitat and provided us an effective standard unit (Cheminée et al 2013). Cheminée (2012) demonstrated that 7 or more 1 m² replicates provide an accurate estimate of juvenile fish densities. The TL of individuals was estimated with the help of fish silhouettes of different sizes (5 mm TL size-classes) on a plastic slate (Macpherson, 1998). Behavior of each fish individual was recorded as one of the 3 attitudes, cryptic, wandering and transitory, which were defined as follow: "Cryptic" individuals were those remaining hidden between thalli at least 30 consecutive seconds and then strictly associated with the canopy, never standing into the open water column (Photo III-2); "wandering" individuals remained less than 30 seconds hidden in the canopy, but remaining wandering inside the plot (Photo III-3); "transitory" individuals would spend only short periods of time in the plot, strictly less than 30 seconds (Photo III-4) (Cheminée, 2012).

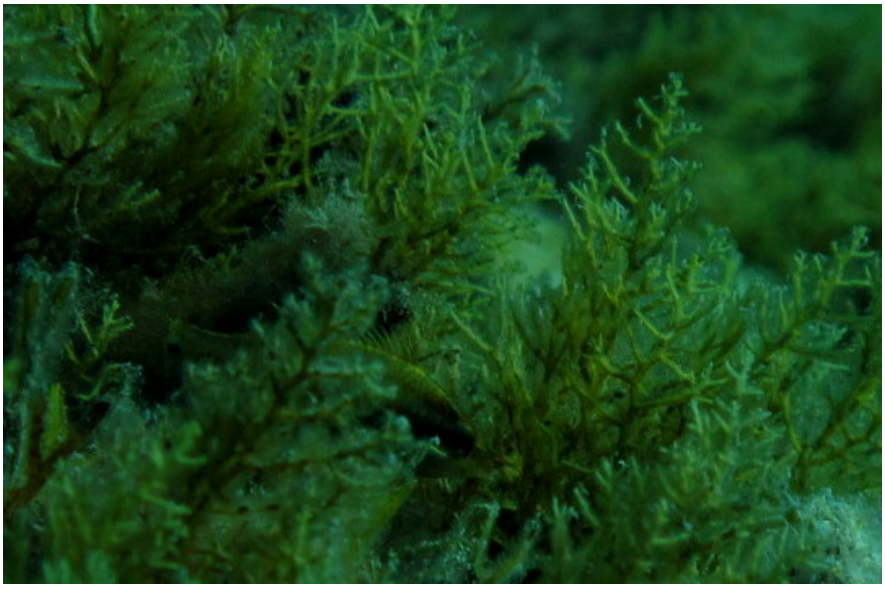

Photo III-2. Cryptic behavior of a juvenile of *Symphodus ocellatus* (45 mm TL, September 2013). Photo: Amalia Cuadros.

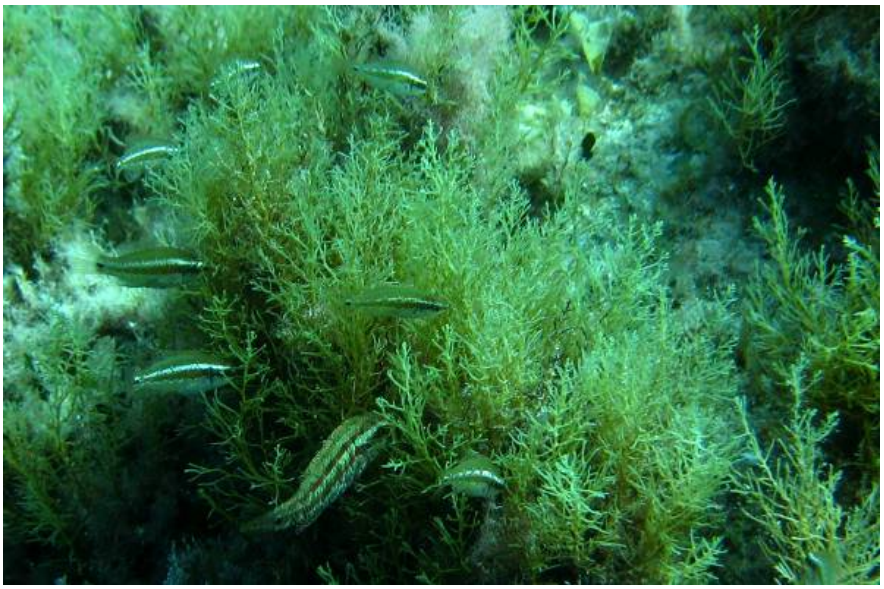

Photo III-3. Wandering behavior of *Symphodus ocellatus* juveniles (30-35 mm TL) and a *Symphodus roissali* (50 mm TL) juvenile (September 2012). Photo: Eva Vidal.

Photo III-4. Transitory behavior of a juvenile of *Serranus scriba* (40 mm TL, July 2010). Photo: Adrien Cheminée.

For each taxa, all individuals smaller than one third of adult maximum total length (Cheminée, 2012; Louisy, 2002) were considered for the juvenile analyses.

Moreover, in order to explore correlation between fish assemblage or taxa specific descriptors and forest structure, *Cystoseira* canopy was described within the same 1m² plots, by using percent coverage and maximum height (to the nearest cm) (Cheminée, 2012).

Some fish species occurred at very low densities and were pooled together for subsequent analyses as follows: *Symphodus* spp. (including *S. roissali*, *S. tinca* and *S. ocellatus*); *Serranus* spp. (including S. *cabrilla* and *S. scriba*); and crypto-benthic species (including different taxa belonging to families Blenniidae, Gobiidae and Tripterygiidae). Afterwards, in order to refer to such groups we denominate them as "taxa". Taxa accounting for more than 10% of the juvenile density of a sampled location were considered as "dominant". All other species or taxa were considered "minority" taxa.

Finally, in 2013, adults were censed by means of UVC, recording their abundance and TL (±1cm) at each site and each depth strata in three replicate belt transects of 10 m x 6 m (Harmelin-Vivien et al., 1985). Fish biomasses were obtained by using the length-weight equations reported by Morey et al. (Morey et al., 2003) in Balearic Islands. For *Thalassoma pavo* and *Oblada melanura* the coefficients reported by Froese & Pauly (2011) in the Atlantic were used because their length-weight relationship were not available for the Mediterranean Sea.

III.2.4. Statistical analyses

Primary we analyzed forest structure to assess its spatial variability among our sampling design drivers. It was analyzed in terms of canopy height, cover and in terms of a single descriptor of three-dimensional forest structure built from both canopy height and cover. Subsequently, we analyzed fish assemblages and taxa-specific descriptors under the influence of both forest structure and our sampling design drivers.

First, we tested if forest structure in terms of canopy height and cover varied (1) between locations, sites and depth strata (with 2012 dataset), and (2) between

protection levels, sites and depth strata (with 2013 dataset), by means of PERMutational univariate Analyses Of Variance (PERMANOVA) (see detailed models in Table III-1).

Both *Cystoseira*-canopy height and cover showed significant variations among sites and across depth strata (see Results section). Furthermore, they were (moderately) correlated (Spearman rank correlation: 0.502< rho <0.293) (see Results section). Consequently a Principal component analysis (PCA) on normalized *Cystoseira* cover and height was performed in order to use the PC1 axis (74.9 and 67.2 % of explained variance for 2012 and 2013, respectively) as a single descriptor of three-dimensional forest structure. Similarly, we tested if the univariate variable PC1 followed similar patterns than *Cystoseira* height and cover (see detailed models in Table III-1).

Secondly, we tested if juvenile assemblages descriptors (total densities, richness and assemblage structure) varied (1) between locations, sites, depth strata and with forest structure (with 2012 dataset) and (2) between protection level, sites, depth strata and with forest structure (with 2013 dataset), by means of univariate and multivariate PERMANOVAs (see detailed models in Table III-1). The considered juvenile assemblage parameters were the univariate total density and richness, and the multivariate assemblage structure (comparative densities of each taxa).

Thirdly we studied taxa specific univariate and multivariate descriptors. To accomplish this objective, only dominant species, with a necto-benthic spatial distribution, were considered. Other dominant species, if planktivores, were not considered (Harmelin, 1987). We tested if univariate densities and TL distributions varied (1) between locations, sites, depth strata and with forest structure (with 2012 dataset) and (2) between protection level, sites, depth strata and with forest structure (with 2013 dataset), by means of univariate PERMANOVAs (see detailed models in Table III-1). Besides we tested if multivariate contingence tables of behavior varied (1) between locations, sites, depth strata, and with TL and forest structure (with 2012 dataset) and (2) between protection level, sites, depth strata, and with TL and forest structure (with 2013 dataset), by means of multivariate PERMANOVAs (see detailed models in Table III-1).

Sums of squares (SS) for these PERMANOVA designs were performed sequentially (type I), the covariates were introduced in the first place into the models (without

including the interaction terms between covariates and factors). It allowed to assess the variations in the response variable(s) that are due to variations in forest structure (i.e. PC1) and/or TL, prior testing the putative effects of location, protection or depth levels (Anderson and Gorley, 2008). Due to colinearity between depth and PC1, when PC1 and depth had both a significant effect on univariate response variables, graphical representations of some linear models' residuals were used. For visualizing the effect of PC1 once the effect of depth were removed, XY biplot was used, where X was PC1 and Y was the residuals of the linear regression fitting the response variable as a function of depth. The effect of depth was visualized in the same way, once the effect of PC1 were removed, XY biplot represented in X depth, and in Y the residuals of the linear regression fitting the response variable as a function of PC1.

Finally, we tested for differences between multivariate adults assemblage structure (here comparative biomass of each taxa) in order to have a global image of adult distribution patterns according to protection, sites and depth strata for the year 2013 (see models details at Table III-1). Afterwards, we tested if univariate densities and TL distributions of predators and con-specifics varied according to protection, sites and depth strata for the year 2013 (see model details at Table III-1). Considered predators were piscivorous species. Considered con-specifics species where the con-specifics of the juvenile dominant species, excluding planktivores.

Table III-1. Univariate and multivariate PERMANOVA models employed with 2012 and 2013 datasets of juvenile fish within *Cystoseira* forests.

Univariate forest models, to test if response variables varied 1) between locations, sites and depth strata (with 2012 dataset); and 2) between protection level, sites and depth strata (with 2013 dataset).		
Response variables	**2012 design factors**	**2013 design factors**
-Canopy height (univariate). -Canopy cover (univariate). -PC1 (univariate).	-Location (fixed, 2 levels (location B and location C)). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in location, 3 levels within each level of the factor location).	-Protection (fixed, 2 levels (inside MPA and outside MPA)). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in protection, 3 levels within each level of the factor protection).
Univariate and multivariate assemblage models, to test if response variables varied 1) between locations, sites, depth strata and with forest structure (with 2012 dataset); and 2) between protection level, sites, depth strata and with forest structure (with 2013 dataset).		
Response variables	**2012 design factors**	**2013 design factors**
-Total juveniles' densities (univariate). -Richness (univariate). -Assemblage structure (multivariate).	-PC1 (covariate). -Location (fixed, 2 levels (location B and location C)). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in location, 3 levels within each level of the factor location).	-PC1 (covariate). -Protection (fixed, 2 levels (inside MPA and outside MPA)). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in protection, 3 levels within each level of the factor protection).
Univariate taxa-specific descriptors models (densities and TL distributions) for dominant species, to test if response variables varied 1) between locations, sites, depth strata and with forest structure (with 2012 dataset); and 2) between protection level, sites, depth strata and with forest structure (with 2013 dataset).		
Response variables	**2012 design factors**	**2013 design factors**
-Taxa-specific densities (univariate). -Taxa-specific TL distributions (univariate).	-PC1 (covariate). -Location (fixed, 2 levels (location B and location C)). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in location, 3 levels within each level of the factor location).	-PC1 (covariate). -Protection (fixed, 2 levels (inside MPA and outside MPA)). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in protection, 3 levels within each level of the factor protection).

Table III-1 (continued)

Multivariate taxa-specific descriptor models for behavior of dominant species, to test if response variables varied 1) between locations, sites, depth strata, and with TL and forest structure (with 2012 dataset); and 2) between protection level, sites, depth strata, and with TL and forest structure (with 2013 dataset).		
Response variables	**2012 design factors**	**2013 design factors**
-Taxa-specific behavior (multivariate).	-TL (covariate). -PC1(covariate). -Location (fixed, 2 levels (location B and location C). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in location, 3 levels within each level of the factor location).	-TL (covariate). -PC1 (covariate). -Protection (fixed, 2 levels (inside MPA and outside MPA)). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in protection, 3 levels within each level of the factor protection).
Multivariate and univariate adult predators descriptor models, to test if response variables varied between protection level, sites and depth strata (with 2013 dataset).		
Response variables	**2012 design factors**	**2013 design factors**
-Assemblage structure (multivariate). -Predator densities (univariate). -Predator TL (univariate). -Con-specifics densities (univariate). -Con-specifics TL (univariate).	Not studied.	-Protection (fixed, 2 levels (inside MPA and outside MPA)). -Depth (fixed, 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m)). -Site (random, nested in protection, 3 levels within each level of the factor protection).

In these analyses P-values were obtained by 999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<200). Terms were pooled as suggested by Anderson et al. (Anderson and Gorley, 2008). Due to the intrinsic variability of ecological data, tests were considered significant for p-values <0.1.

Additionally, for the juvenile assemblage structure analyses, two complementary multivariate exploratory approaches were used: a nMDS biplot of samples and a SIMPER test. By analogy to the use of correlation circle with PCA, we used arrows superimposed to nMDS biplots for representing the spearman rank correlations between

biplot axes and taxa densities and forest structure (PC1). SIMPER test was used as analysis of species contributions to significant differences between sets of samples (Clarke and Warwick, 2001). SIMPER test were employed too for description of adult assemblages.

For multivariate inferential and exploratory analyses of densities we used Binomial deviance dissimilarities (an improvement of the Bray-Curtis measure according to Anderson & Millar (2004)); Multivariate behavior composition (proportions) were analyzed through Sogard resemblance matrix, which is an alternative to the Chi-squared measure of distance (Clarke and Warwick, 2001). Univariate data (density or TL) were analyzed with Euclidian distances.

Exploratory analyses and inferential tests were performed using the PRIMER 6 and PERMANOVA + B20 package (Anderson and Gorley, 2008; Clarke and Gorley, 2006). Graphical visualizations were performed in R Environment (R Development Core Team, 2013) using the library ggplot2 (Wickham, 2009).

III.3. RESULTS

III.3.1. Effect of location, protection and depth on forest descriptors

In 2012, height and percentage cover of *Cystoseira* canopy were in average about (±se) 8.29 cm (±3.35) and 75.86% (±10.88), respectively; in 2013 in average about 8.99 cm (±2.87) and 74.47% (±11.53), respectively. Both height and percentage cover showed significant spatial variations across depth strata, although magnitude of the depth effect varied significantly among sites (PERMANOVAs, Si(lo)xde $p<0.05$, see Supplementary data, Table VIII-1). Canopy height and cover increased with depth in most of the sites, in both 2012 and 2013, with d2 displaying intermediary values, but in some cases similar to d1 and in others to d3 (pair-wise results in Supplementary data, Fig. VIII-1). Additionally, there were statistically significant differences in *Cystoseira* height at larger spatial scales, between locations in 2012 and between inside and outside MPA in 2013; but this was not the case for *Cystoseira* cover. Furthermore, a weak but positive correlation between *Cystoseira* height and cover was found in both years (2012: rho=

0.502, p<0.001; 2013: rho=0.293, p<0.001). Thus, a PCA with both normalized *Cystoseira* cover and height was executed in order to obtain a new variable (i.e. PC1 axis) as a single descriptor of the forest three-dimensional structure. PC1 increased with depth or presented d3 displaying intermediary values, or similar values to d1 depending on sites (pair-wise results in Fig. III-2). Furthermore, PC1 displayed significant differences between locations in 2012 and between protection levels in 2013 (PERMANOVAs p<0.05, Table VIII-1 of Supplementary data, and pair-wise results in Fig. III-2). Location-depth or Protection-depth interaction was not significant in any case for *Cystoseira* height, cover or PC1.

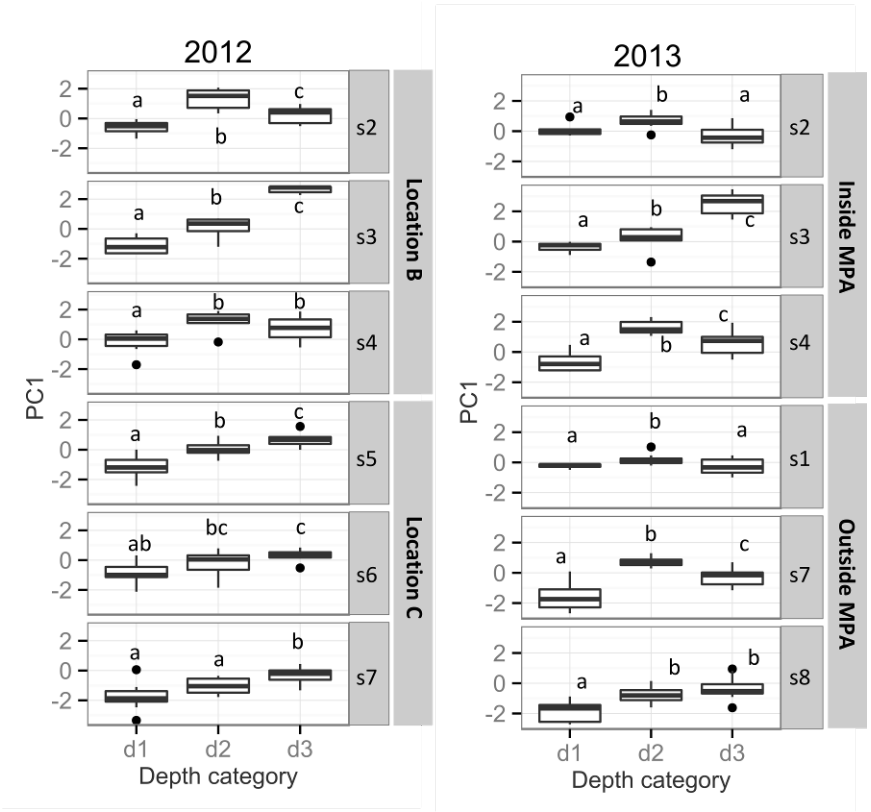

Fig. III-2. Boxplots of *Cystoseira* forest structure (PC1 axis) within samples according to locations (2012)/ protection (2013), depth categories (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m) and sites. Box plots indicate the median (bold line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the inter quartile range (whiskers), and remaining outliers (open circles). Pair-wise tests between treatments are given in box plots (different lower case characters indicate significant differences between treatments).

III.3.2. Effect of habitat structure, location, protection and depth on juvenile fish assemblage trends

III.3.2.1.Total density and richness

For fish juveniles, a total of 9 and 11 taxa were observed in 2012 and 2013 respectively (Table III-2).

Table III-2. Juvenile fishes observed in *Cystoseira* forests in 2012 and 2013: total number (n), dominance categories, mean TL (mm ± se), minimum (Min) and maximum (Max) TL (mm). Total sampled area per year = 288 m².

	2012					2013				
Species	Dominance	n	Mean TL ± se	Min TL	Max TL	Dominance	n	Mean TL± se	Min TL	Max TL
Chromis chromis	minority	15	50.33±0.33	50	55	dominant	205	37.05±0.51	30	50
Coris julis	dominant	192	43.25±0.68	10	65	dominant	237	42.13±0.65	20	60
Diplodus sargus	minority	54	67.41±1.91	25	90	minority	51	74.41±1.14	60	90
Diplodus vulgaris	minority	36	50.56±5.21	10	90	minority	39	76.92±1.38	50	90
Oblada melanura	minority	5	58.00±10.08	40	85	dominant	270	43.43±0.56	30	90
Sarpa salpa	not recorded	0	-	-	-	minority	38	82.11±1.42	70	100
Seriola sp.	not recorded	0	-	-	-	minority	21	280±0.00	280	280
Serranus spp.	minority	5	82.00±3.74	70	90	minority	45	71.78±1.72	50	90
Symphodus spp.	minority	29	36.72±2.14	20	60	dominant	271	34.02±0.57	20	60
Thalassoma pavo	dominant	268	36.08±0.75	10	60	dominant	443	24.55±0.43	10	60
Blenniidae-Gobiidae-Tripterygiidae	minority	33	38.64±0.73	30	45	minority	17	37.94±1.29	25	45

Globally, the total density and the taxonomical richness of the juvenile fish assemblage were not affected by depth and did not differ between locations or protection levels at any time (Fig. III-3). Only richness in 2012 displayed significant depth-site interaction (PERMANOVA, $p<0.05$, Table VIII-2 of Supplementary data) but with ambiguous pattern in the pair-wise tests. Location-depth or Protection-depth interaction was not significant in any case for total density or richness.

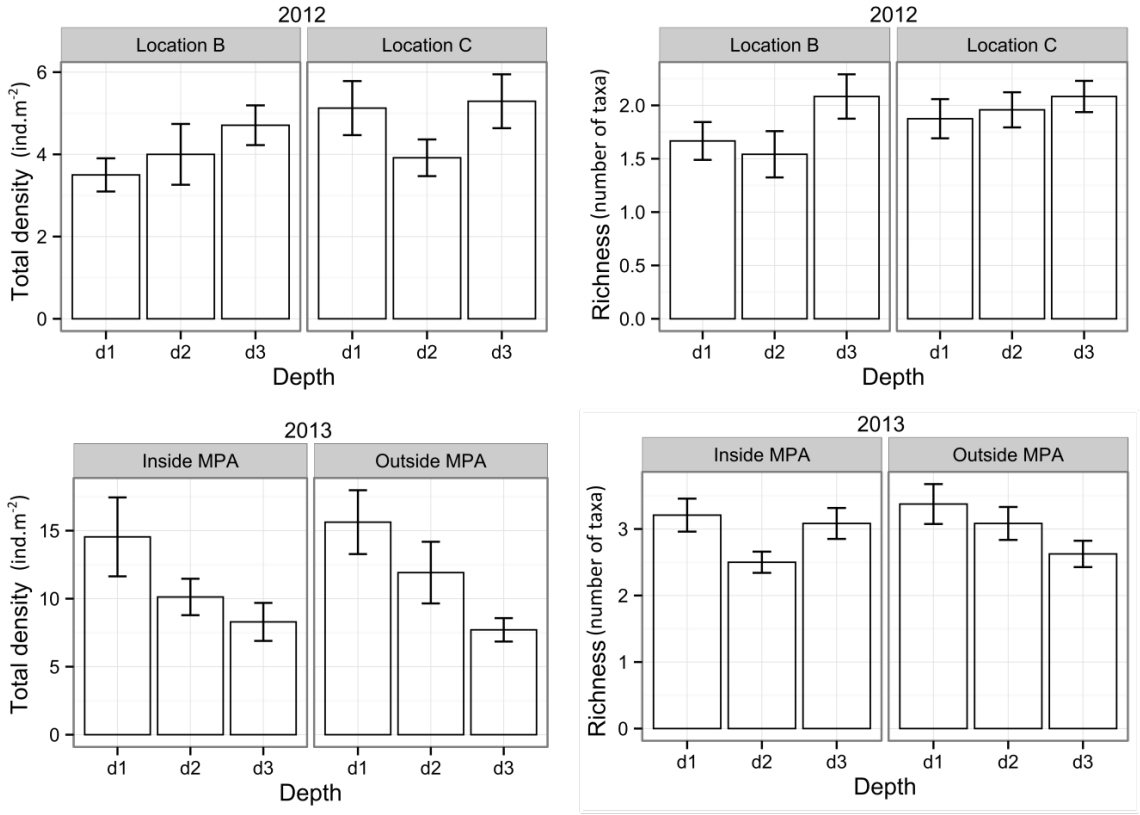

Fig. III-3. Barplots of mean total density and mean richness in *Cystoseira* forests within samples according to locations (2012) / protection (2013) and depth categories (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m). Barplots include error bars (=s.e.).

III.3.2.2. Assemblage structure

The structure of the juvenile assemblage did not differ between locations or protection levels. However, it was significantly affected by depth and forest structure (PC1) in both years (Table III-3, Fig. III-4, Fig. III-5). Depth effects varied significantly among sites. However, almost all sites displayed a different assemblage between d1 and d3, with intermediary patterns for d2, where assemblage was similar to d1 or d3 depending on sites.

Table III-3. PERMANOVA table of results: influence of *Cystoseira* forest structure (PC1), location (2012), protection (2013) and depth on the multivariate descriptor of juvenile fish assemblage (juvenile fish assemblage structure). Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. *P*-values were obtained by 999 permutations of residuals under a reduced model.

2012				
Source of variation	Df	MS	Pseudo-F	P(perm)
PC1	1	31.29	26.85	**0.001*** **
Location (lo)	1	5.56	2.66	0.104
Depth (de)	2	12.85	5.18	**0.004** **
Site (si(lo))	4	2.27	2.73	**0.007** **
loxde	2	0.39	0.16	0.885
si(lo)xde	8	2.54	3.05	**0.001*** **
Residuals	125	0.83		
Total	143			
2013				
Source of variation	Df	MS	Pseudo-F	P(perm)
PC1	1	52.95	13.27	**0.001*** **
Protection (pr)	1	5.65	0.65	0.843
Depth (de)	2	35.64	7.92	**0.001*** **
Site (si(pr))	4	9.70	5.22	**0.001*** **
prxde	2	3.98	0.90	0.515
si(pr)xde	8	4.30	2.31	**0.003** **
Residuals	125	1.86		
Total	143			

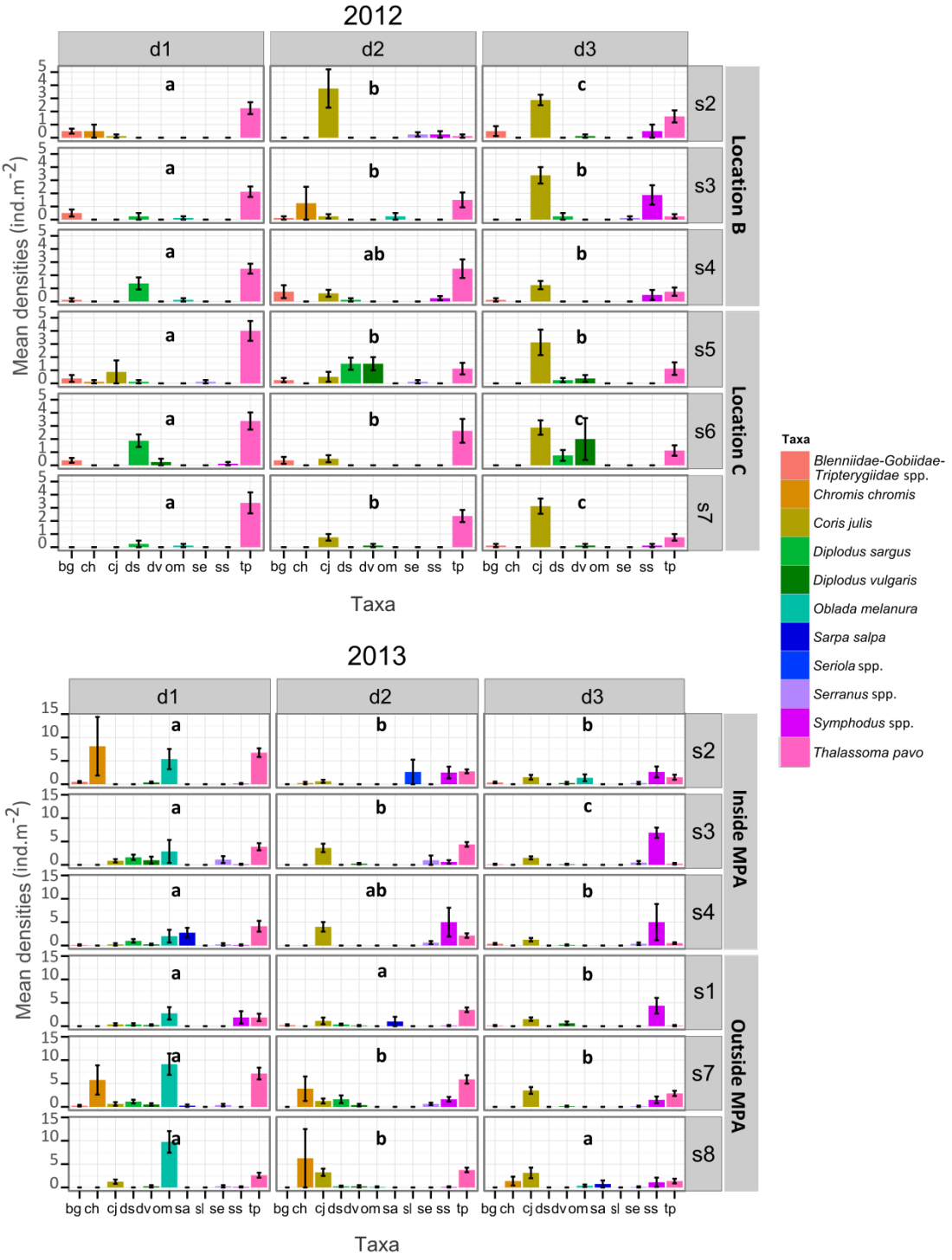

Fig. III-4. Juvenile assemblage in *Cystoseira* forests for each depth (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m, in 2012 and 2013) in each site ; mean juvenile densities (ind.m^{-2}) per taxa. Note that the y-axis scale vary between graphs. bg= Blenniidae-Gobiidae-Tripterygiidae spp.; ch= *Chromis chromis*; cj= *Coris julis*; ds= *Diplodus sargus*; dv= *Diplodus vulgaris*; om= *Oblada melanura*; sa= *Sarpa salpa*; sl= *Seriola* spp.; se= *Serranus* spp.; ss= *Symhodus* spp.; tp= *Thalassoma pavo* – error bares = s.e. Pair-wise tests between treatments are given (different lower case characters indicate significant differences between depths at a given site. The pair-wise results should be read horizontally).

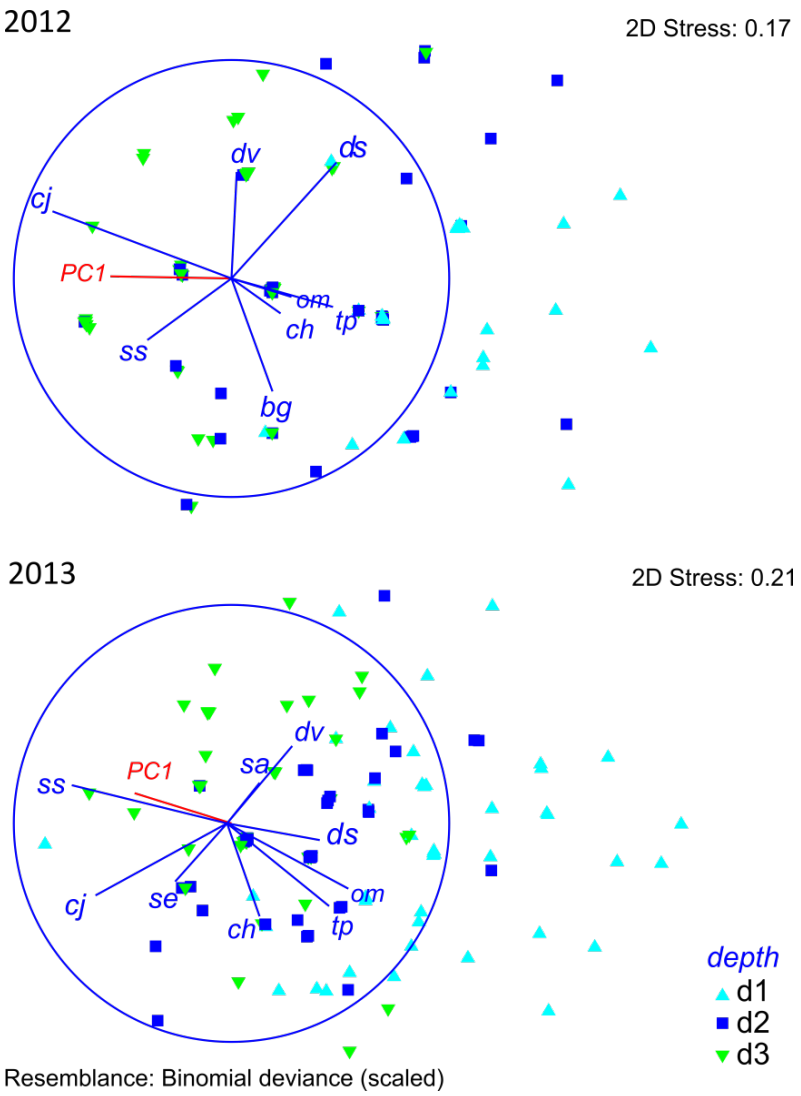

Fig. III-5. nMDS ordination plot of fish juvenile assemblages within *Cystoseira* forests for both sampling years according to depth strata (from the shallowest d1 to the deepest d3; d1: 3-5 m, d2: 6-8 m, d3: 10-12 m). Correlation vectors (Spearman) of forest structure (PC1, in red) and taxa specific densities (in blue) are plotted (for correlations >0.2). Taxa: ch= *Chromis chromis;* bg=Blenniidae-Gobiidae-Tripterygiidae; dv= *Diplodus vulgaris;* ds= *Diplodus sargus ;* cj= *Coris julis;* om= *Oblada melanura;* sa= *Sarpa salpa;* se= *Serranus* spp.; ss= *Symphodus* spp.; tp=*Thalassoma pavo*. PC1: forest structure (= forest height and cover).

Depth-related variations of juvenile fish densities are highlighted in the nMDS ordination plots (Fig. III-5). Multivariate differences in juvenile fish densities between depth strata were primarily driven by *Thalassoma pavo* and *Coris julis* in both years, as well as by *Oblada melanura* and *Symphodus spp* but only in 2013 (SIMPER analysis, Table I-4). *T pavo* and *O. melanura* densities tended to decrease with depth, while *C. julis* and *Symphodus* spp. densities tended to increase with depth (Fig. III-4, Fig. III-5, see also Fig. III-6 in the next section 'taxa specific').

Table III-4. Results obtained with the similarity analysis (SIMPER) of *Cystoseira* forest juvenile assemblage data between groups of assemblages according to depth d1, d2 and d3.

Year	Depth	Depth dissimilarity (%)	Contribution of species to dissimilarity (%)
2012	d1-d3	79.48	*Coris julis* (39.55), *Thalassoma pavo (32.49).*
	d1-d2	66.81	*Thalassoma pavo (45.31), Coris julis* (18.30), *Diplodus sargus* (13.47)
	d3-d2	72.86	*Coris julis* (41.92), *Thalassoma pavo (27.07).*
2013	d1-d3	83.74	*Oblada melanura* (24.21), *Thalassoma pavo* (21.90), *Symphodus spp.*(18.54), *Coris julis* (12.28).
	d1-d2	71.09	*Oblada melanura* (25.84), *Thalassoma pavo* (18.82), *Coris julis* (14.77), *Symphodus spp.*(10.33).
	d3-d2	70.59	*Symphodus spp.*(27.13), *Thalassoma pavo* (26.63), *Coris julis* (20.02).

III.3.3 . Effect of habitat structure, location, protection and depth on juvenile taxa specific trends

III.3.3.1. Density of the dominant taxa

The taxa-specific density of the dominant taxa (not planktivores) *C. julis*, *Symphodus* spp. and *T. pavo*, were not affected by locations or protection levels at any time. Neither location-depth or protection-depth interactions were significant.

C. julis densities significantly differed between depth strata in both years. Although depth effects varied significantly among sites, most of sites presented an increase of *C. julis* density from shallower to deeper depth strata, with intermediary densities for d2, which in some cases were similar to d1 and in others to d3. Independently of depth, *C. julis* density also significantly decreased with PC1 values, but only in 2012 (Fig. III-6A, PERMANOVAs in Table VIII-3 of Supplementary data). *T. pavo* densities significantly decreased according to both depth and PC1 the two years, although the pattern according to PC1 was clearer in 2012. Depth effects varied significantly among sites, but most of sites presented a decrease of *T. pavo* density from shallower to deeper depth strata, with intermediary patterns for d2, which were similar to d1 or d3 according to sites (Fig. III-6B, Table VIII-3 of Supplementary data). Finally, *Symphodus* spp., which were abundantly observed only in 2013, significantly increased in density according to both depth and PC1 (Fig. III-6C, Table VIII-3 of Supplementary data).

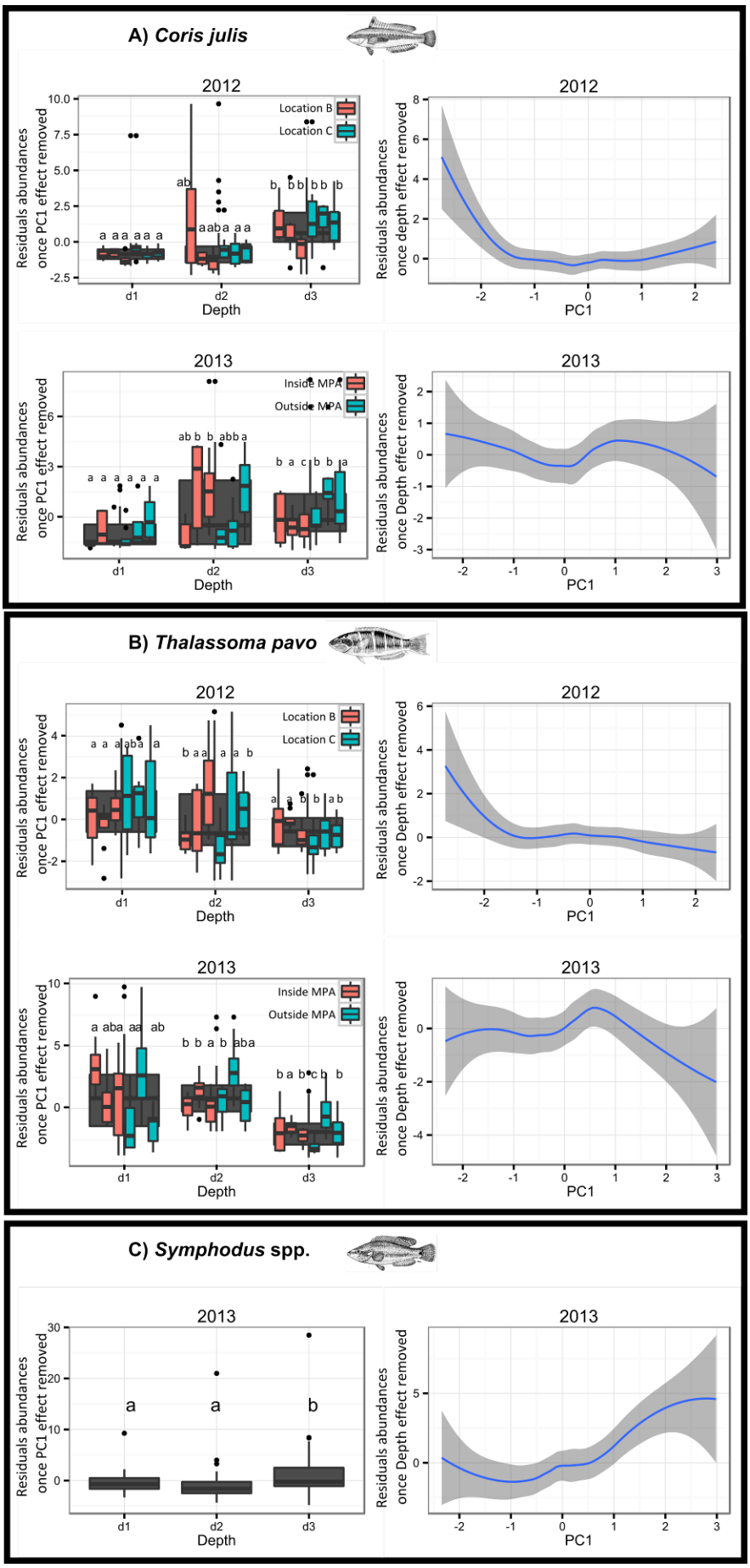

Fig. III-6. Respective effects (disentangled) of depth (Boxplots in left panels) and the *Cystoseira* forest three-dimensional structure variable PC1 (smoothed curves in right panels) on densities of the dominant juveniles: A) *Coris julis*, B) *Thalassoma pavo*, C) *Symphodus* spp. (see M & M section).
Box plots indicate the median (bold line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the inter quartile range (whiskers), and remaining outliers (open circles). Shadow areas of curves represent s.e. Pair-wise tests between treatments for boxplots are given (different lower case characters indicate significant differences between treatments). Depth categories are: d1: 3-5 m, d2: 6-8 m, d3: 10-12 m.

III.3.3.2. Total lenght (TL) distributions of the dominant taxa

The taxa-specific TL of *C. julis* and *T. pavo* were not affected by locations or protection levels at any time. Neither *C. julis* nor *T. pavo* TL display a clear pattern according to depth. However a significant influence of PC1 on *T. pavo* TL was consistent in the two years, although the pattern was clearer in 2013 (Fig. III-7). For *C. julis* TL, tests were not possible in 2012 due to the low number of individuals in the shallower depths. *C. julis* TL decreased according to depth outside reserve in 2013, but not inside reserve. *T. pavo* TL also decreased according to depth but only in 2012. *T. pavo* TL decreased significantly both years according to PC1; although it was less evident in 2012 (PERMANOVAs and pair-wise tests, Fig. III-7, and Table VIII-4 of Supplementary data,). *Symphodus* spp. TL patterns tests were not possible due to the low number of individuals in the shallower depths.

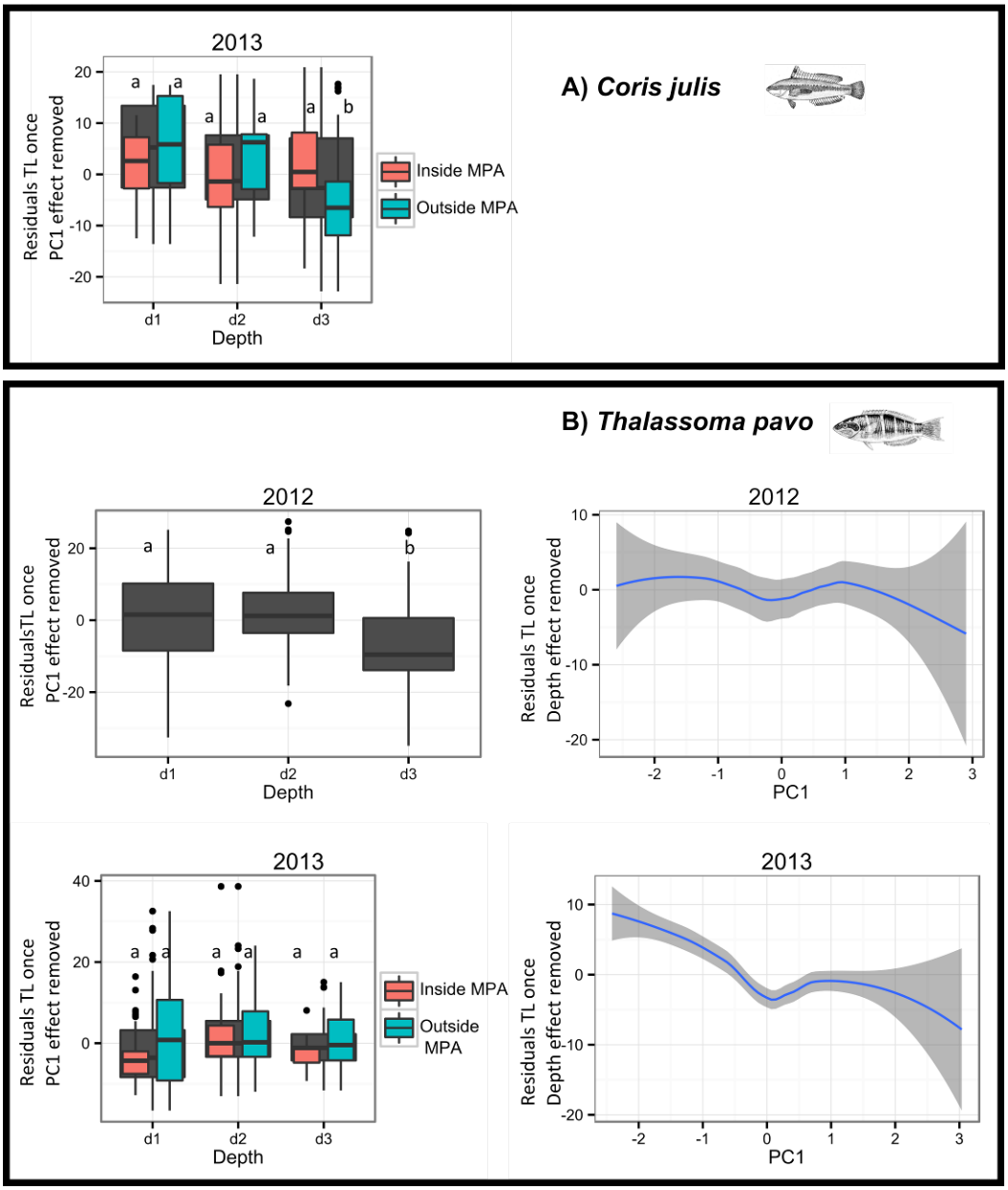

Fig. III-7. Boxplots and smoothed curves of residuals of mean TL (mm) of the dominant juveniles in *Cystoseira* forests once PC1 or depth linear model residuals were removed (in order to discern depth and PC1 influence on mean TL tendencies). Considered taxa: A) *Coris julis* (in 2013), B) *Thalassoma pavo* (in 2012 and 2013) (see M & M section and Fig. III-6). Pair-wise tests between treatments are given in box plots (different lower case characters indicate significant differences between treatments). Depth categories are: d1: 3-5 m, d2: 6-8 m, d3: 10-12 m.

III.3.3.3. Behavioral traits of the dominant taxa

The taxa-specific behavior of *C. julis* and *T. pavo* were not affected by locations or protection levels at any time. Location-depth or protection-depth interaction was not significant or did not display clear patterns.

Both *C. julis* and *T. pavo* showed significantly more cryptic-wandering behavior for their smaller sizes, and they become more transitory as they gain size. Furthermore, *T. pavo* showed both years a significant effect of forest structure (PC1) on its behavior, as more complex forest favored a more cryptic behavior. Besides, depth-site interaction was significant for *T. pavo* behavior in 2012, but behavior patterns according to depth were inconsistent among sites. For *C. julis* in 2012 and for *Symphodus* spp., behavior tests were not possible due to the low number of individuals in the shallower depths (Fig. III-8, PERMANOVAs, see Table VIII-5 of Supplementary data).

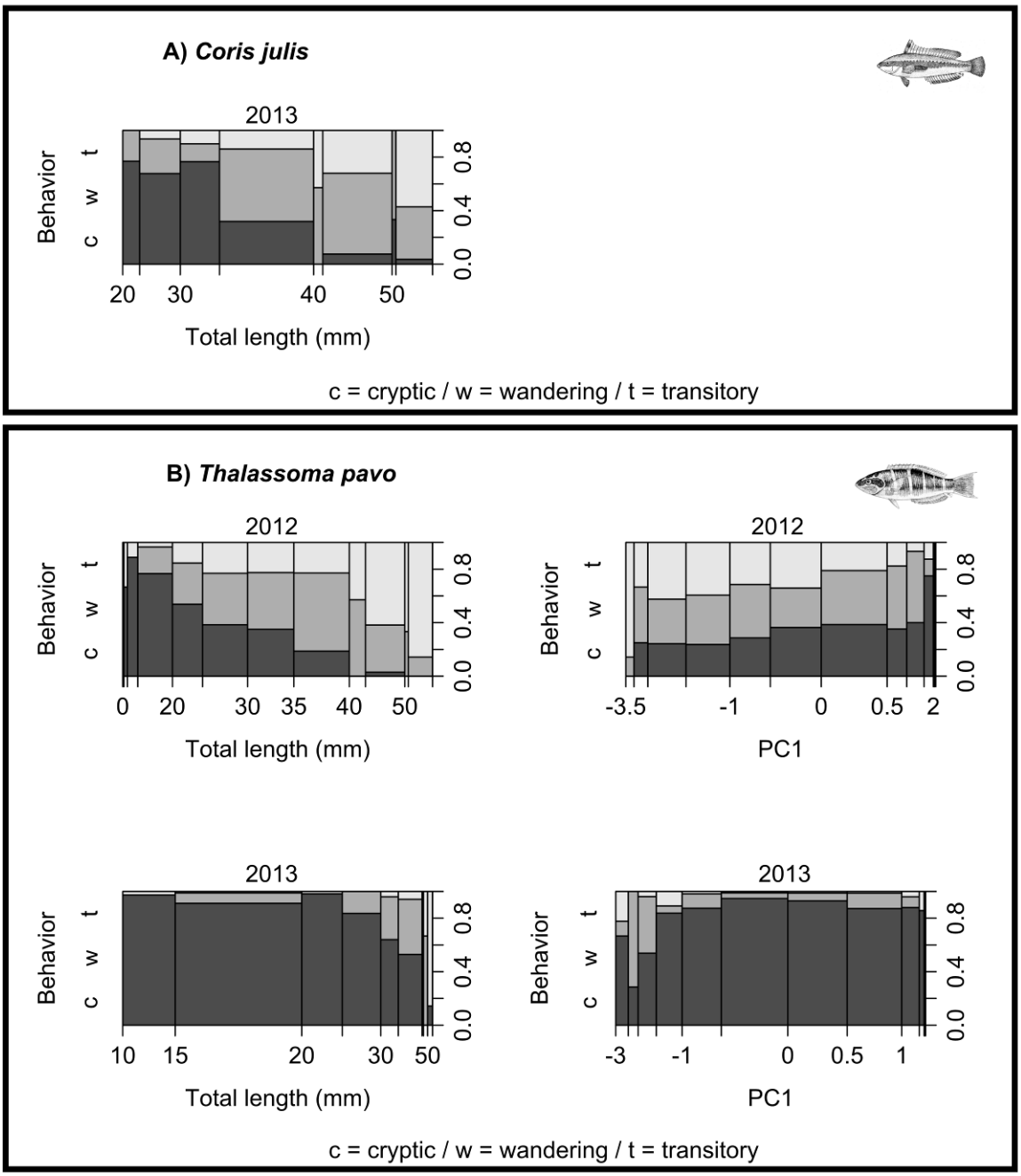

Fig. III-8. Proportion of each behavior type according to significant terms for each considered dominant taxa in *Cystoseira* forests. Behavior types: c, cryptic; w, wandering; t, transitory. Considered taxa: A) *Coris julis* (in 2013); B) *Thalassoma pavo* (in 2012 and 2013).

III.3.4. Effect of protection and depth on adult trends

The adult assemblage structure didn't display any effect of the protection level, neither protection-depth interaction. However, adult assemblage varied with depth (PERMANOVA, F=2.47, p=0.04; Fig. III-9, Table III-5, and Supplementary data: Table VIII-6, and Table VIII-7). The average of Bray-Curtis dissimilarities was the highest

between pairs of depths d1 and d3. The main species which typify each depth and explained up to 70% of the dissimilarity between pair samples were: *Sarpa salpa*, *T. pavo*, *Symphodus* spp., *C. julis* and *Serranus* spp. (SIMPER test, Table III-5).

Table III-5. Results obtained with the similarity analysis (SIMPER) of *Cystoseira* forest adult assemblage data in terms of biomass between groups of assemblages according to depth d1, d2 and d3.

Year	Depth	Depth dissimilarity (%)	Contribution of species to dissimilarity (%)
2013	d1-d3	68.31	*Sarpa salpa (20.91%)*, *Thalassoma pavo (19.10%)*, *Symphodus* spp. (16.06%), *Serranus* spp. (12.17%), *Coris julis* (11.51%)
	d1-d2	64.17	*Sarpa salpa (25.40%)*, *Coris julis (17.06)*, *Symphodus* spp. (15.41%), *Thalassoma pavo (14.51%)*.
	d3-d2	58.43	*Symphodus* spp. (19.88%), *Sarpa salpa (18.66%)*, *Coris julis* (17.44%).

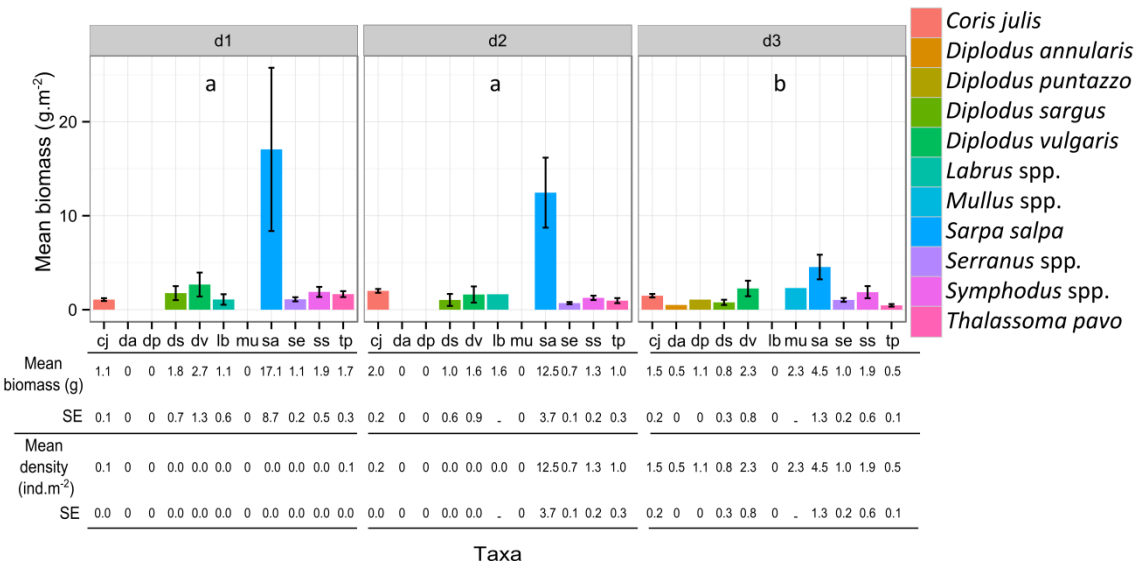

Fig. III-9. Mean adult biomass in *Cystoseira* forests for each depth, per taxa ($g.m^{-2}$); cj= *Coris julis*; bg= Blenniidae-Gobiidae-Tripterygiidae spp.; da= *Diplodus annularis*; dp= *Diplodus puntazzo*; ds= *Diplodus sargus*; dv= *Diplodus vulgaris*; lb= *Labrus* spp.; sa= *Sarpa salpa*; se= *Serranus* spp.; ss= *Symphodus* spp.; tp=*Thalassoma pavo* – error bares = s.e. Depth categories are: d1: 3-5 m, d2: 6-8 m, d3: 10-12 m. Pair-wise tests between treatments are given in bar plots (different lower case characters indicate significant differences between treatments). Depth categories are: d1: 3-5 m, d2: 6-8 m, d3: 10-12 m. Data set of 2013.

Density of possible predators of juveniles, represented in these observations only by *Serranus* spp., were very low and didn't differ between protection or depth levels; the protection-depth interaction was not significant (PERMANOVA, $p>0.1$). TL distributions varied according to depth-site interaction, however pair-wise tests didn't display a clear pattern among sites (Supplementary data Table VIII-6).

Density or TL of *C.julis* adults didn't display any effect of the protection level. Protection-depth interaction was not significant. However depth-site interaction was significant for *C. julis* densities and TL (PERMANOVA, $p<0.05$): densities tended to increase with depth in most of sites (PERMANOVA, pair-wise $p<0.1$ in every sites). TL did not display any clear patterns along depth in the different sites (see Supplementary data Table VIII-6 and Table VIII-7 for more details).

Density or TL of *Symphodus* spp. didn't display any effect of the protection level or depth, and protection-depth interaction was not significant (PERMANOVA $p>0.1$) (see Supplementary data Table VIII-6 and Table VIII-7).

Density or TL of *T.pavo* didn't display any effect of the protection level. Protection-depth interaction was not significant (PERMANOVA $p>0.1$). However, density decreased with depth (PERMANOVA, $F= 4.93$, $p<0.01$). Depth effect was not significant for *T. pavo* TL (PERMANOVA $p>0.1$).

III.4. DISCUSSION

The structure of the *Cystoseira* forests at northern Minorca varied between sites distributed a few hundred of meters apart, between locations distributed tens of kilometres apart, and also between locations situated inside and outside the MPA. This pattern may respond to differences in substrate type (carbonated, non-carbonated) and sun exposure, rather than to trophic cascades caused by protection, because the biomass of adjoining trophic levels, fish invertebrate-feeders, sea urchins, and erect algae, are uncorrelated in the *Cystoseira* forests of northern Minorca, either inside and outside the MPA (Cardona et al. 2007b; Cardona et al., 2013). Furthermore, forest structuration increased with depth: it might be related notably to a decrease of the biomass and grazing intensity of the herbivorous fish *Sarpa salpa* as depth increases (Tomas et al., 2005; Vergés et al., 2009). On the other hand, the composition of the juvenile fish assemblage differed between sites a few hundred of meters apart and changed with depth, but did not vary at a larger geographic scale or between locations situated inside and outside the MPA. These results suggest that the structure of the juvenile assemblage is related to both depth and forest structure but that the factors structuring juveniles assemblages operate at an intermediate spatial scale of hundreds of

meters. The results reported here confirm that the fish density distribution patterns are tightly related to the *Cystoseira* forest structure. But more structured forests may not necessarily favor all the fish species and size classes.

The density of juvenile *C. julis* and *T. pavo* decreased sharply in highly structured forests, whereas the highest density of juveniles of *Symphodus* spp. were observed in such more complex forests. These observations are in agreement with those of a previous study which also reported the association of juvenile *C. julis* with sparse forests and that of juvenile *Symphodus* spp. to denser forests (Cheminée, 2012).

Higher shelter availability (Cheminée, 2012; Riccato et al., 2009; Thiriet et al., 2014) and higher food supply for juvenile fishes (Chemello and Milazzo, 2002; Pitacco et al., 2014; Thiriet et al., 2014) have been suggested to increase the nursery value of dense *Cystoseira* forests. A trade-off between safety and foraging efficiency often exists for fishes and hence the optimal habitat optimizes low predation risk and higher food availability (Dahlgren and Eggleston, 2000). Shelter is particularly critical for juvenile fishes, because of their small size and high vulnerability to predators (Sogard, 1997) and hence cryptic behavior has been widely reported in the bibliography as a response to predation risk in juvenile fishes (Lehtiniemi, 2005; Shulman, 1985; Valdimarsson and Metcalfe, 1998). This may be also true for juvenile *Symphodus* spp. of any size and for the smallest juveniles of *C. julis* and *T. pavo*. On the other hand, the species considered here prey upon small invertebrates (Guidetti, 2004; Kabasakal, 2001; Thiriet et al., 2014) which may be more abundant in sparse *Cystoseira* forests, than in denser ones, at least gastropods and small sea urchins (Bonaviri et al., 2012; Kelaher, 2003), due to intense predation by hermit crabs, shrimps and other micro-predators (Bonaviri et al., 2012) in denser forests. In this scenario, dense forests certainly offer more shelter but sparse forests offer more food.

In this apparent opposite scenario, the contrasting preferences in microhabitat use reported here for the juvenile *C. julis*, *T. pavo versus Symphodus* spp. may be explained by differences in morphology of fish. It allows fish to achieve a good avoidance of predators and to feed efficiently, independently of their preferred distribution on sparse or dense forest. This morphological differences are in terms of color patterns and locomotory efficiency due to differences in body shape (Hertel, 1966; Motta et al., 1995; Schmid and Senn, 2002). Juvenile *Symphodus* spp. are pale brown, which provide them with great camouflage in the canopy. On the contrary, juvenile *C. julis* and *T. pavo* have more

colourful patterns and hence less cryptic. Furthermore, a compressed, sub-gibbose body, with long and pointed pectoral fins and a subterminal mouth is typical of mobile and manoeuvrable epibenthic foragers inhabiting complex habitats whereas streamlined fishes are better adapted for fast swimming (Hoar and Randall, 1979; Keast and Deirdre, 2011; Motta et al., 1995; Recasens et al., 2006). *Symphodus* spp. have a much deeper body that *C. julis* and *T. pavo* which may favour their movements within the canopy and explain why the former are often observed in association with structurally complex habitats (Bussotti and Guidetti, 2010). Whereas *C. julis* and *T. pavo* are more streamlined, favouring their mobility in less complex habitats. Consequently, *Symphodus* spp. are able to manoeuvre in complex habitat, favouring their foraging efficiency, but are slower, relying more on shelter for escaping from predators. Whereas, *C. julis* and *T. pavo* are less able to manoeuvre in complex habitats, forced to explore less structured habitats, but faster, relying more on their speed to reach refuges for escaping from predators.

Hence, it is not surprising that juvenile *Symphodus*, independently of body length, usually displayed a cryptic behavior and were abundant in the most complex forests; whereas *C. julis* and *T. pavo* are related with sparser forests (Cheminée, 2012). As regards to juvenile total length, cryptic behavior also prevailed in the smallest juveniles of *C. julis* and *T. pavo* and the highest density of small juveniles of *T. pavo* were also found in the denser forests. Furthermore, the juveniles of *T. pavo* displayed a more cryptic behavior in dense forests, whereas in the less complex forests they switched towards wandering or transitory behaviors. However, as both species grew up, they moved towards sparser forests and shifted to a wandering or transient behavior, probably as their swimming speed increased, allowing them to adventure further from refuges.

Unfortunately, the results reported here do not allow to test the possible influence of predator and con-specific density inside and outside MPAs on the density of juveniles, as no differences were observed in the density of adult predators and con-specifics between sites inside and outside the MPA. Fish protection at the MPA of northern Minorca has resulted into a higher biomass of species vulnerable to spear fishing such as *Diplodus* spp. (Cardona et al., 2013; Coll et al., 2012) but not into a higher biomass of adult labrids and predators of juvenile, such as *S. scriba* (Cardona et al., 2013, 2007b). This is because none of the most abundant fish species found in this study is a target for commercial fisheries in the Balearic Island (Morales-Nin et al., 2005) and because recreational angling from small boats may certainly reduce their abundance locally but usually only in much deeper water

than the depth strata surveyed here (Cardona et al., 2007a). However, con-specific *C. julis* and *T. pavo* adult densities varied with depth, but displayed similar spatial patterns than juveniles, discarding a spatial partition of resources for avoiding competence between adults and juveniles and supporting the absence of evident ontogenetic shifts in bathymetry during the life history of these species (Guidetti and D´Ambrosio, 2004).

Depth also influenced the juvenile fish assemblage composition and taxa specific density in our study, as in previous works (Francour, 1997; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Vigliola and Harmelin-Vivien, 2001). However, unclear tendencies were found for taxa specific length distributions and behavior trends according to depth. Thus, assemblage composition but not species richness or total density, changed with depth, mainly because of the opposing trends of *C. julis* and *T. pavo*. Shallow assemblages were characterized by higher densities of *T. pavo* while deeper assemblages displayed greater density of *C. julis.* These depth patterns are in agreement with previous studies, where juveniles of *T. pavo* are mainly found in shallow waters, whereas *C. julis* juveniles dwell in deeper waters (García-Rubies and Macpherson, 1995; Guidetti and D´Ambrosio, 2004). Additionally, for both species, no patterns of TL was observed according to depth, even more confirming previous results that suggested the absence of evident ontogenetic shifts in bathymetry during the life history of these species.

In summary, in agreement with the habitat quality trade off hypothesis (i.e. the highest quality habitat minimizes mortality rate by offering the trade-off between foraging and safety (Dahlgren and Eggleston, 2000), we can hypothesize that dense forest provides both shelter and food to juvenile *Symphodus* spp. of any size and for very small juveniles of *C. julis* and *T. pavo*. As they grow, predation risk of juvenile might decrease as their body-size increase (refuge in size, maybe due to, at least in part, increase in velocity and manoeuvrability, preponderant ability in escaping attacking predators). This might allow large fish to spend less time hidden (cryptic) and to spend more time for foraging activity (wandering & transitory). Consequently, the nursery value of dense *Cystoseria* forests may vary among species. Whether such habitat preference is due to real active choice of the most favorable habitat (Dahlgren and Eggleston, 2000) or is due to differential mortality, remains still unclear (Thiriet et al., 2014). Finally, although juveniles of these three taxa (*T. pavo*, *C. julis*, *Symphodus* spp.) could be found in *Cystoseira* forests, inter-specific competition may be reduced by differences in microhabitat use. Indeed, *Symphodus* spp. may prefer complex forests, whereas *T. pavo* and *C. julis* both prefer sparse forests, the

T. pavo in shallow water and the *C. julis* in deeper areas, thus avoiding competition between them (Guidetti and D´Ambrosio, 2004). Such spatio (and also temporal) partition of resources for juveniles (refuge, food) has been also highlighted in others habitats (Harmelin-Vivien et al., 1995).

III.5. CONCLUSIONS

As a conclusion, the effect of protection could not be tested, since commercial or recreational fisheries do not operate at the depth strata considered and consequently no differences in studied adult distributions were found inside *versus* outside MPA. However, variations of depth and of forest structure had additive effects explaining changes in fish juvenile assemblages. On one hand, depth determined a taxa-specific distribution; on the other hand, habitat structure affected juvenile fish assemblages notably by inducing behavioral changes. We argue that the optimum production of juveniles of different species in such seascapes is acquired through the intrinsic patchy nature of forests, displaying a mosaic of various habitat characteristics, and therefore fulfilling the contrasted needs of different species. Future protection and management measures, as well as restoration projects, should take these outcomes into account in order to optimize management efforts. Thus, adequate spatial management strategies should act at a seascape scale and require a protection of a mosaic of various habitat types, including each of them with their own heterogeneity.

Chapter IV. Effect of weather conditions on the settlement and recruitment of *Diplodus sargus* in Minorca

Photo IV-1. North coast of Minorca island. Photo: Amalia Cuadros.

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Chapter IV. Effect of weather conditions on the settlement and recruitment of *Diplodus sargus* in Minorca

IV.1. INTRODUCTION

IV.1.1. Context of the study

Chapters II and III focused on the influence of seascape attributes, at various spatio-temporal scales, on juvenile fishes. Here in Chapter IV, we introduced a new potentially driving factor: the hydrodynamics.

Many benthic marine organisms, belonging to multiple phyla, present a bipartite life cycle consisting of an initial pelagic phase in which eggs and larvae are dispersed by currents and a second and more site-attached phase in which juveniles develop into adults (Thresher et al., 1989; Vigliola et al., 1998). The replenishment of their populations is largely dependent on the transition process to the benthic environment, called settlement, and from the subsequent development within benthic areas, where juveniles already adapted to a necto-benthic life are growing and getting ready to join adult populations in a process called recruitment (Connell, 1985; Levin, 1994; Macpherson, 1998; Vigliola and Harmelin-Vivien, 2001). Two metrics allow to measuring the density of juveniles at these two sequential steps: the settlement success and the recruitment level. The “settlement success” is the maximum number of recently settled individuals, also referred to as “settlement peak” or “settlers peak density”. The “recruitment level” is the number of juveniles remaining after an arbitrary period of time following the main settlement event (Cheminee et al., 2011; Macpherson et al., 1997; Macpherson and Zika, 1999).

Environmental variables related with hydrological conditions, such as currents, wind velocity and direction, flood tides, lunar cycles and water temperatures influence settlement rates, but the magnitude of their influence differs among species, space and time and remains subject to considerable uncertainty ((Raventos and Macpherson, 2005), and references therein).

In spite of this, hydrodynamics are often considered one of the most influencing factors on larval dispersal and hence determining the spatial distribution and the availability of larvae near settlement sites, i.e., the larval supply in a specific area (Asplin et al., 1999; Bell et al., 1988; Cowen, 2002; Cowen and Sponaugle, 2009; Hannan and Williams, 1998; Jenkins et al., 1997; Peck et al., 2012) at a given time (Bertness et al., 1996; Brown et al., 2005; Garland et al., 2002; Jacinto and Cruz, 2008; Shanks and Brink, 2005). Dispersal can take place over large spatial scales (Di Franco et al., 2012) but local larval retention is also possible, as suggested by some studies based on modelling, otolith microchemistry, tagging and genetic markers (Cowen et al., 2006; Sponaugle et al., 2002). Once near settlement sites, larval supply is a constraining variable for settlement, since without larval supply, there is no settlement (Pineda et al., 2010). After larval supply is accomplished, flow velocities and turbulence determine settlement success for some organisms (Pineda et al., 2010). However, the influence of local flow velocities and turbulence in fish settlement has been less studied. Additionally, in the case of fish the influence of hydrodynamics on dispersal, larval supply and subsequent settlement may be modulated by the fish themselves. Primarily by spawners, through their distribution and reproduction-strategies, e.g. spawning often takes place associated with major current systems. And secondly by larvae, through larval swimming and orientation capabilities (Berumen et al., 2012; Bradbury et al., 2008; Gerlach et al., 2006; Montgomery et al., 2006; Mouritsen et al., 2013; Norcross and Shaw, 1984).

On the other hand, although the role of hydrodynamic processes on dispersal, larval supply and settlement for different organisms has been investigated for over five decades (e.g. Crisp (1955), the influence of hydrologic changes on post-settlement stages has been less studied (Lassig, 1983), and research has been usually more focused on the effects of high-magnitude environmental events (Walsh, 1983). In coastal necto-benthic fish species intense post-settlement mortality is often considered a demographic bottleneck determining the strength of a cohort which will be eventually incorporated into an adult population (Caley et al., 1996; Doherty and Fowler, 1994; Sano, 1997). However, there are still many uncertainties about the relative contribution of settlement and recruitment on the replenishment of adult populations (Caley et al., 1996; Félix-Hackradt et al., 2013b). Providing information about the relative contribution of these processes, and how they are affected by different environmental and biological factors on them is a pivotal issue.

The white seabream *Diplodus sargus* is one of the most abundant fishes in sublittoral rocky bottoms in the Mediterranean Sea (Sala et al., 2012). They spawn planktonic eggs in spring and larvae spend approximately 28 days among the plankton, close to the sea surface, until settlement, when body length is about 10 mm (Vigliola, 1998). Settlement habitat is limited to shallow (<2 m depth) gently sloping coves with mixed heterogeneous substrata of sand, pebbles and rocks (Photo IV-II) (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). Although post-settlement growth and survival is density dependent (Planes et al., 1999), the influence of hydrodynamics on their settlement and post-settlement is poorly known.

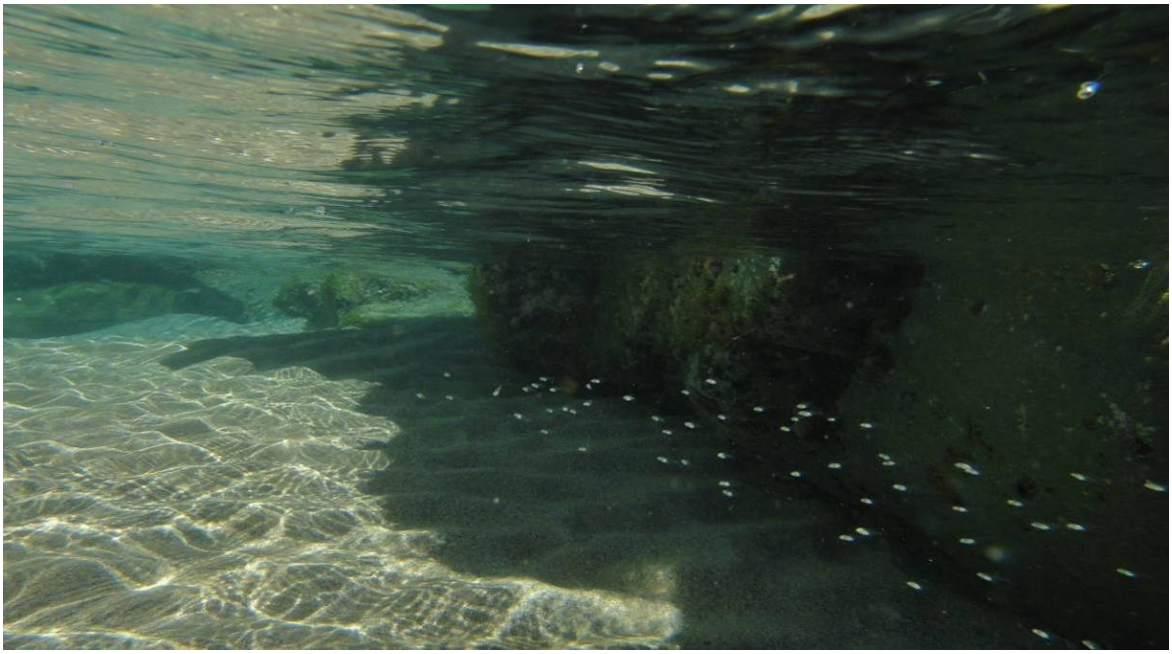

Photo IV-2. Nursery habitat of *Diplodus sargus***.** *D. sargus* settlers: 10-15 mm Total Length (Minorca island, depth= 0.5 meters, April 2012). Photo: Amalia Cuadros.

IV.1.2. Objectives of Chapter IV

The present chapter analyses settlement and post-settlement processes of white seabream within nursery habitats, assessing the arrival of settlers, their subsequent growth, mortality rates and recruitment level in relation to hydrological variables (hydrodynamics and water temperature). Our aim is to improve the knowledge on the relative contribution of such factors in structuring fish populations, which is essential for management and conservation purposes of coastal fish species.

IV.2. MATERIAL AND METHODS

IV.2.1. Studied area

As in the rest of the Balearic Archipelago, coastal circulation in Minorca is mainly regulated by wind forcing (Balaguer et al., 2007; Canellas Moragues, 2010). Forcing by tides is almost negligible in the Mediterranean Sea. Breeze conditions are prevalent for most of the warm season, a regime that is occasionally disrupted by Tramontana episodes, a northerly wind with strong intensity (Llompart et al., 1979). The West-East elongated orientation of the island (approximately 44 and 17 km long and wide respectively) and the dominant northerly winds create two well defined hydro-dynamical areas, the more exposed northern coast, exposed to the strongest storm episodes, and the sheltered southern coast (Llompart et al., 1979).

IV.2.2. Sampling design

The study focused on two locations, placed on the northeast and the southwest coast of the island (here named respectively NE and SW locations), and was performed at six coves (three per location) characterized by the presence of suitable microhabitats for the settlement of white seabream (Fig. IV-1). Juveniles were monitored once or twice a week in 2012, from the 23th of April to the 20th of July, in order to encompass the whole settlement period (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). The three coves within each location were always monitored during the same sampling day, and always under suitable weather conditions.

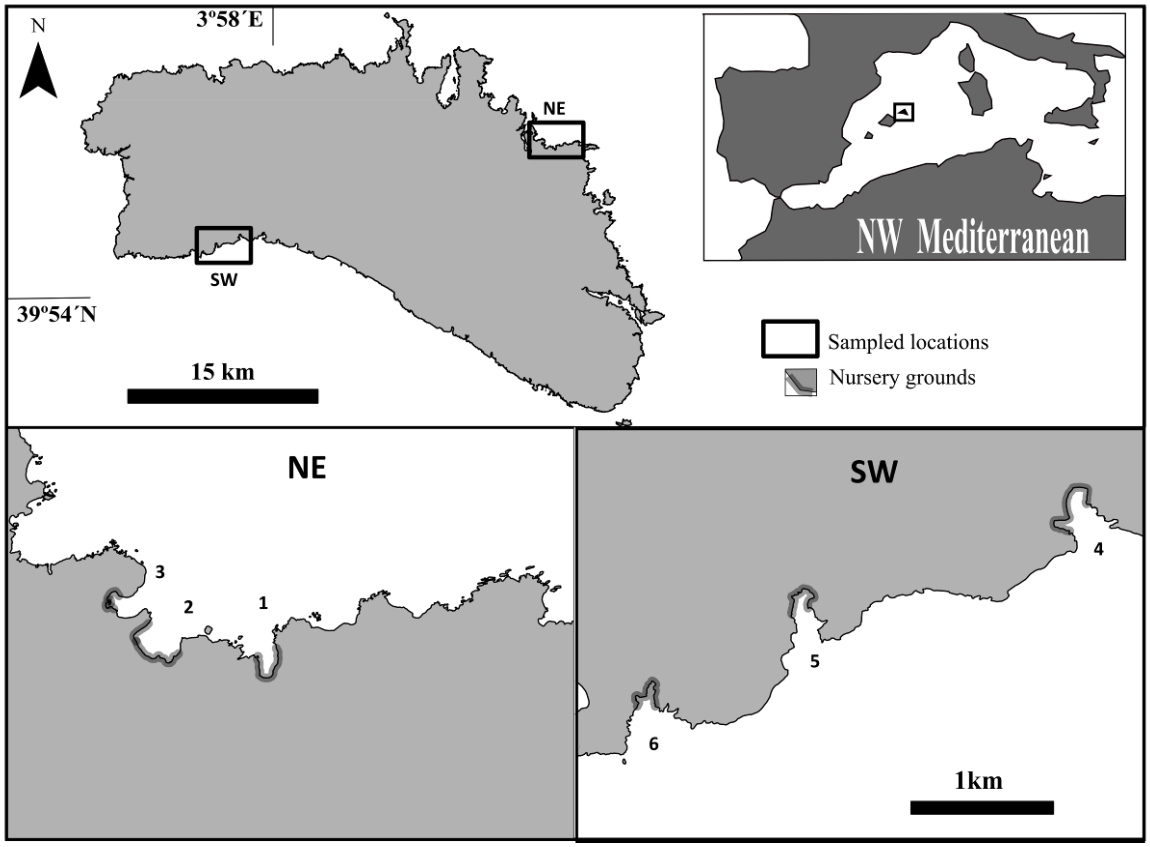

Fig. IV-1. The two distinct sampling locations and the six sampled coves of Chapter IV.
Sampling locations= black squares. Coves included in the northeast location (NE): 1= "Calderer" (39º59´45.34" N, 4º13´45.78" E), 2= "S´Enclusa" (39º59´50.61" N, 4º13´11.26" E), 3= "Mongofre" (40º0´0.53" N, 4º13´3.14" S); and in the southwest location (SW): 4=" Macarella" (39º56´12.02" N, 3º56´13.71" E)., 5= "Turqueta" (39º55´56.28" N, 3º54´54.04" E), 6= "Es Talaier" (39º55´33.43" N, 3º54´7.71" E).

IV.2.3. Data collection

Abundance and size of white seabream juveniles were assessed by means of Underwater Visual Censuses (UVC) (Harmelin-Vivien et al., 1985). At each cove, juveniles were counted and size estimated along pre-defined transects running parallel to the shoreline (55 meters mean length) and covering the entire cove. The beginning and end of each transect were referred to some topographical features of the coastline, to ensure accurate repeatability overtime independent of the observer. Censuses were carried out by two previously calibrated observers, who snorkelled slowly at depths ranging from 0.5 to 3 m. Only juvenile fish were recorded, i.e. individuals from 10 mm to 100 mm total length (TL) (Table IV-1). Their total length (TL) was estimated with the help of fish silhouettes of different sizes pictured on the slate (5 mm TL size-classes from 10-15 mm to 80-85 mm TL) (Cheminee et al., 2011; Cheminée et al., 2013; Pastor et al., 2013; Vigliola et al., 1998). The precision of this size estimating method is ± 3.5 mm for *Diplodus* species

(Macpherson, 1998). All UVC were performed between 10 am and 4 pm. For subsequent statistical analyses fish densities were standardised to one linear meter of shoreline (Cheminee et al., 2011; Harmelin-Vivien et al., 1985).

Table IV-1. Census of *Diplodus sargus* juveniles for Chapter IV. Number of sampling days (NSD), effective transects (ET), total number (TN) of *Diplodus sargus* juveniles censed during the study period, maximum juveniles censed per day (MNJ) and size ranges (total length, TL) recorded at each cove. The shoreline length of the coves (SL), and their location (NE: northeast, SW: southwest) are also indicated.

Cove	SL	Location	NSD	ET	TN	MNJ	TL
Calderer	451.5 m	NE	16	112	22432	5589	10-85 mm
S´Enclusa	606 m	NE	17	182	41986	6148	10-65 mm
Mongofre	622.45 m	NE	17	184	28833	4926	10-65 mm
Es Talaier	408.69 m	SW	15	132	21281	5150	10-85 mm
Turqueta	324.95 m	SW	15	89	21271	2844	10-85 mm
Macarella	540.16 m	SW	15	154	36386	3347	10-90 mm

Wave and wind data were provided by *Puertos del Estado* (Puertos del Estado, 2015). These parameters were monitored at two buoys: placed northeast (SIMAR-44-2083040: 40.00° N, 4.38° E), and southwest (SIMAR-44-2079039: 39.88º N, 3.88º E), of the study area, respectively. Additionally, at each cove, sea surface temperatures were recorded during the entire study using an Onset HOBO Water Temp Pro v2 sensor placed on the sea bottom at 5 m depth.

IV.2.4. Statistical analyses

IV.2.4.1. Physical forcing

A correlation matrix between all physical variables obtained from buoys and HOBO sensors was constructed to check for collinearity-redundancy in environmental variables considering the data recorded during census days and 5 days prior to each census. This was done because fish censuses were carried out the days with better meteorological conditions, in order to assure an accurate count of fish inside the nursery. Using 5-days averages allowed to better characterise the environmental conditions occurring among consecutive sampling days. The environmental variables included in the correlation matrix are detailed in Table IV-2. Since temperature displayed the highest range of variation, we selected the less variable parameter (miT). For the other less variable parameters, we used mean values.

Colinearity between environmental variables was assessed by means of the Variation Inflation Factor (VIF). A cut-off VIF value of 3 was applied to reduce the number of environmental variables in the model (Zuur et al., 2009). Thus, variables with a value higher than 3 were excluded from further analyses. The final correlation matrix was constructed with the set of variables selected by VIF, but persistent correlated variables or variables with redundant information were excluded. Finally, temporal variations in the ultimate-selected variables were compared between both locations (NE vs. SW) by means of Spearman rank correlation analysis.

Table IV-2. List of the environmental and biological parameters considered in the Chapter IV. The environmental variables include data registered during the same census days ("x") and the average of the 5 days prior to each census ("x5").

Environmental parameters		Biological parameters	
Date	Julian date	MD	Mean density
miT, miT5	Minimum temperature	PP	Maximum population peak
P, P5	Wave Period	DP	Date of maximum PP
Dwa, Dwa5	Wave Direction	RL	Recruitment level
Hwa, Hwa5	Wave height	ID	Population density increase
Hwi; Hwi5	Wind waves height	DD	Population density decrease
Swi. Swi5	Wind speed	MTL	Mean total length
Dwi, Dwi5	Wind direction		

IV.2.4.2. Juvenile population dynamics

A. Juvenile population descriptors

The different informative parameters calculated to describe juvenile population dynamics are detailed in Table IV-2. The 80-90 % of individuals of the maximum PP ranged between 10-15 mm TL and consequently was considered as a proxy of the settlement peak (Cheminee et al., 2011). Recruitment Level (RL) referred to the number of juveniles remaining at the end of the sampling period after the main settlement event.

Increases in population density (ID) were calculated from the initial sampling date until the day of PP, while decreases (DD) were calculated from this date until the last sampling date. ID and DD were analysed for the whole population taking into account that ID was mainly shaped by smaller individuals, which had recently arrived at the nursery (85-95% were individuals ranging from [10, 20) mm TL), and DD was mainly shaped by individuals

which were incapable of leaving the nursery (individuals with a TL lower than 40 mm (Vigliola 1998)). TL increase rates were calculated by means of daily mean TL (MTL), from the first to the last sampling day.

The relationship between the response variables ID DD and MTL and Date were analyzed by means of least square regression analyses. Analyses of covariance (ANCOVA) was used to compare the slope of the regression lines by testing the effect of cove (included as a categorical factor in the model) on juvenile density (ID and DD) and MTL, as dependent variables, while adjusting for the effect of Date considered as a continuous covariate. The assumptions involved in the regression analyses were checked in terms of residuals (Christensen, 1996). Tukey HSD post-hoc comparisons between coves were performed for ID, DD and MTL when appropriate.

B. Influence of physical forcing in juvenile dynamics

Once population dynamics were described, the influence of physical forcing on the spatio-temporal variation of juvenile mean density and life history (i.e., MTL trends), was analysed by means of Generalized Additive Modelling (GAM) (Hastie and Tibshirani, 1990). GAMs are nonparametric regressions with the main advantage of not requiring a prior specification of underlying non-linear functional forms between dependent and independent variables. Thus, the data tell us what shape the functional relationships have (smooths).

Physical forcing variables initially included in the GAM analyses were those previously selected by VIF analysis and correlation criteria. Additionally, the GAM model applied to analyse the variability in MTL included population densities (log-transformed, lD) as a factor to tackle for possible density-dependence processes (Planes et al., 1999). Wave and wind directions (0º-360º) were incorporated as circular variables in the models. Due to the large number of environmental variables considered in this study, a best-final models selection was applied based on the minimization on the generalized cross validation (GCV). The GCV of a model is a proxy of the out-of-sample predictive mean squared error (Wood, 2000). It penalizes a large number of parameters in the model and therefore, a model with lower GCV has more explanatory power, and hence is preferred, to a model with higher GCV. Degrees of freedom of the smooth terms (i.e. number of knots) were

then estimated by minimizing the GCV (Wood, 2003, 2004). We used variations of the GAM formulations, as implemented in "mgcv" (R Development Core Team, 2013) (i.e. GAMs with GCV smoothness estimation (Wood, 2003, 2000)). A step-forward selection was applied starting with all the covariates initially included in the models, removing one non-significant covariate at a time. We also included an interaction effect of each covariate per cove. After the series were fitted, residuals were checked for homogeneity of variance and violation of normality assumptions.

IV.3. RESULTS

IV.3.1. Physical forcing variability

VIF analysis evidenced colinearity between factors Date and miT, because water temperature increased as the warmer season went on (Fig. IV-2). Furthermore, miT was correlated with miT5. Factors Hwa-Hwi and Hwa5-Hwi5 were respectively correlated with Swi and Swi5, because the height of waves or wind waves increased with wind speed. Factors Hwa and Hwa5 were correlated with P and P5, respectively, indicating that the waves with the smallest period were usually the highest ones. Accordingly, and to avoid colinearity, factors Date, Tmi5, Hwa, Hwi, Hwa5 and Hwi5 were excluded from the dynamics analyses. A correlation matrix was built with the remaining factors, namely: miT, P, Dwa, Swi, Dwi, P5, Dwa5, Swi5 and Dwi5. Wave and wind directions (Dwa-Dwa5; Dwi-Dwi5) were moderately correlated, because wave directions were determined by wind blowing directions. Therefore, they were considered redundant and only wind direction was used for further analyses. P5 was highly correlated with Swi5, since wave period is a consequence of both wind speed and its blowing duration; thus, for further analyses period parameters (P-P5) were removed. In conclusion, in the end, only miT, Swi, Dwi, Swi5 and Dwi5 were considered for analyses (Fig. IV-2):

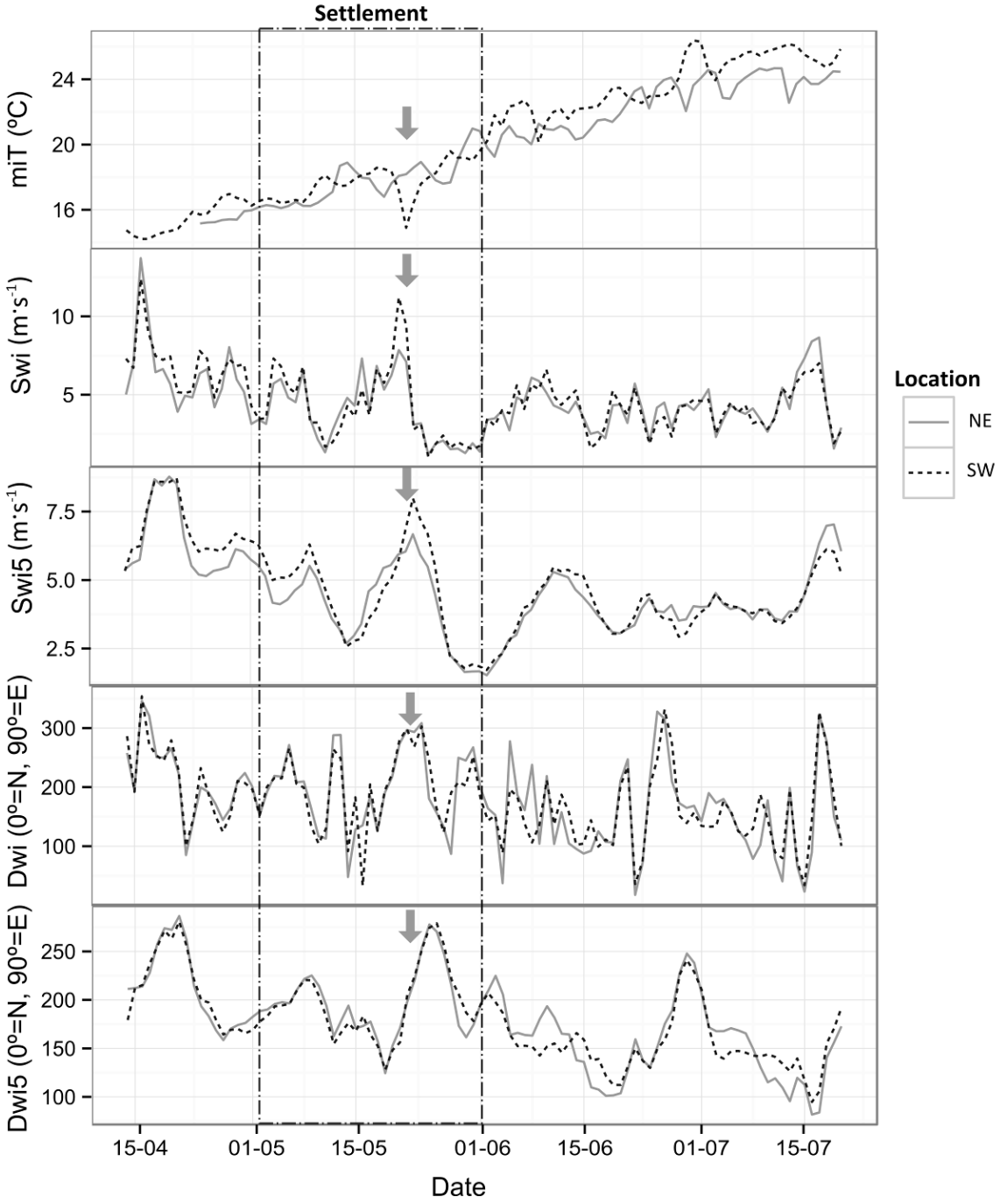

Fig. IV-2. Temporal variation of the selected environmental parameters recorded by NE (northeast) and SW (southwest) buoys and HOBO sensors during the sampling period. miT: minimum temperature (ºC), Swi: wind speed ($m.s^{-1}$), Swi5: wind speed for the 5 day period ($m.s^{-1}$), Dwi: wind direction (0°=North, 90°=Est) and Dwi5: wind direction for the 5 day period (0°=North, 90°=Est). The dotted frame represents the interlude where *Diplodus sargus* settlement occurs. Arrows indicate the rough hydrodynamic event which occurred during *Diplodus sargus* settlement.

Variations in miT, Swi, Dwi, Swi5 and Dwi5 occurred relatively synchronized between NE and SW locations and presented a high correlation ($r > 0.5$). Representations of waves and winds during the period of study showed various “rough hydrodynamic events”, but

only one of them (characterized by winds of 10 $m.s^{-1}$ from SE , and corresponding waves higher than 1.5 m, with periods of 10 s) overlapped with settlement, in the middle of May (Fig. IV-3).

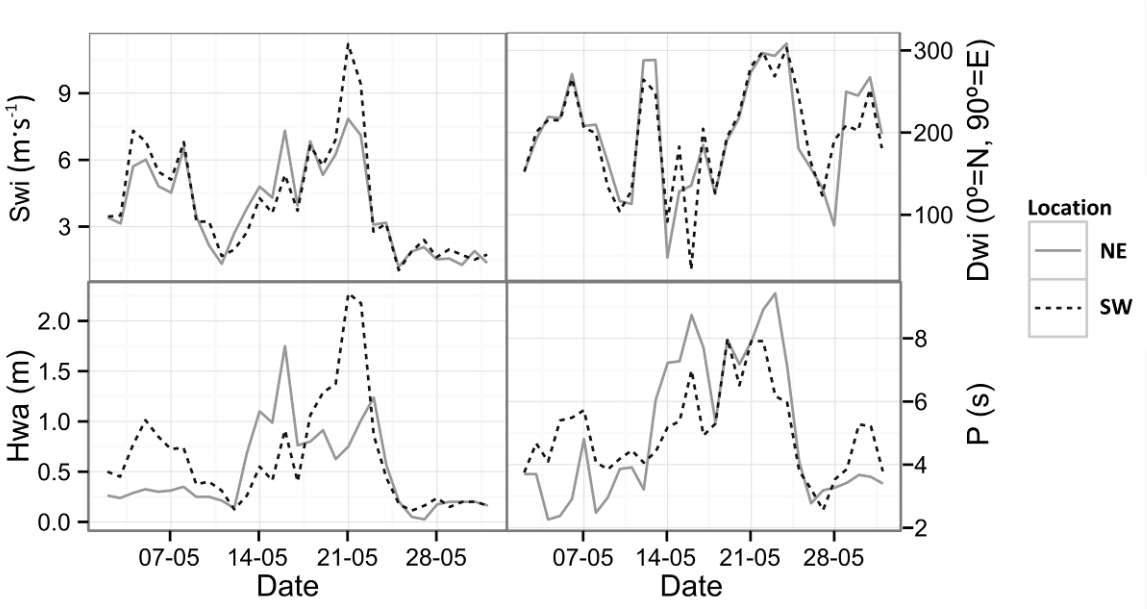

Fig. IV-3. Temporal variation of environmental parameters in May, illustrating the rough hydrodynamic event as recorded by NE (northeast) and SW (southwest) buoys during *Diplodus sargus* settlement. Swi: wind speed ($m.s^{-1}$), Dwi: wind direction (0°=North, 90°=Est), H: wave height (m), P: wave period (s).

IV.3.2. Juvenile population dynamics and influence of physical forcing

IV.3.2.1. Temporal and spatial variation of juvenile population descriptors

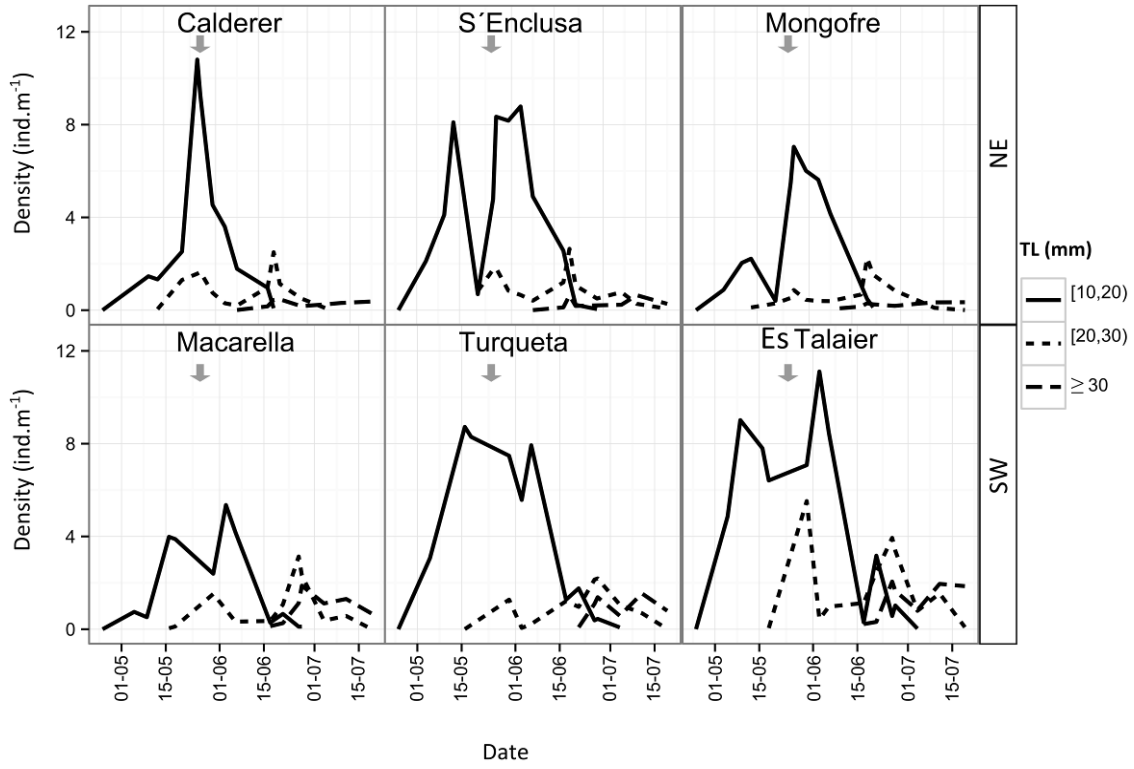

Fig. IV-4. Temporal patterns of *Diplodus sargus* density at each cove and location NE (northeast) and SW (southwest). Fish density is represented independently for three different size classes: [10,20) mm; [20,30) mm and individuals larger than 30 mm TL. Density (ind.m^{-1}), TL: Total length (mm). Arrows indicate the rough hydrodynamic event during settlement.

Changes in juvenile density over time were highly synchronized at the six coves (Fig. IV-4). Density of juveniles shorter than 20 mm ([10, 20) mm) increased dramatically everywhere in early May, decreased in late May and peaked again in early June, except in Calderer, where density did not increase again in June. Actually, the late May decline in density was much larger in the NE coves than in the SW ones. A bimodal pattern was still obvious for the 20-30 mm size class ([20,30) mm); although juvenile density decreased sharply everywhere as they grew larger and density peaks were delayed two weeks when compared with those of the 10-20 mm size class (Fig. IV-4). Individuals ≥40 mm accounted only for 1 to 5 % of the juvenile population.

Despite the above reported similarities in phenology, coves often differed in fish density (Fig. IV-4, Table IV-3). MD at each cove ranged from 2.535 ± 0.525 ind.m^{-1} (in Macarella) to 5.935 ± 0.968 (in Es Talaier). PP ranged from 6.196 ind.m^{-1} (in Macarella) to 12.379 (in Es Talaier) and took place by the end of May for all coves. RL was apparently higher in coves from the SW location, where it ranged from 0.541 to 1.568 ind.m^{-1}. At the NE location RL ranged from 0.280 to 0.394 ind.m^{-1}.

Table IV-3. Juvenile *Diplodus sargus* population dynamic parameters obtained at coves situated in the NE (northeast) and SW (southwest) locations, respectively. MD: mean density ± standard error; PP: population peak; PD: population peak date; RL: recruitment level (considered as the number of juveniles remaining in the nursery on the last sampling date). D[10,20), D[20,30), D≥30 are mean density ± standard error of individuals of TL [10,20), [20,30), and ≥30 mm, respectively. MD, PP, RL and D[10,20), D[20,30), D≥30 are expressed as individuals per meter of shoreline (ind.m^{-1}).

	NE			SW		
Cove	Calderer	S´Enclusa	Mongofre	Macarella	Turqueta	Es Talaier
MD	3.105 ± 0.916	3.696 ± 0.799	2.725 ± 0.609	2.535 ± 0.525	4.364 ± 0.761	5.935 ± 0.968
PP	12.379	10.15	7.9139	6.196	8.752	12.601
PD	24/05/2012	25/05/2012	25/05/2012	01/06/2012	28/05/2012	28/05/2012
RL	0.284	0.394	0.280	0.541	0.686	1.568
D[10,20)	2.276 ± 0.836	3.186 ± 0.822	2.094± 0.612	1.482 ± 0.494	3.342 ± 0.894	3.989 ± 1.035
D[20,30)	0.690 ± 0.191	0.753 ± 0.184	0.520 ± 0.146	0.712 ± 0.244	0.654 ± 0.202	1.355 ± 0.445
D≥30	0.139 ± 0.044	0.136 ± 0.052	0.111 ± 0.034	0.432 ± 0.161	0.368 ± 0.145	0.592 ± 0.21

The increase in population densities (from the first sampling date until the PD), the decrease in population densities (from the PD until the last sampling day) and the increase in MTL for the whole sampling period for each cove are shown in Fig. IV-5. The ANCOVA results comparing the regression lines between coves for ID, DD and MLT and Date indicate that no significant differences existed between the slopes for any of them (Table IV-4). By contrast, significant differences were found in ID and DD intercepts among coves, but not for MTL. For ID, higher density values were found in Es Talaier and significant differences were found between Es Talaier and Macarella and between the former and Mongofre. For DD, higher density values were also obtained in Es Talaier, while significant differences were found between this cove and the rest, except for S'Enclusa. Significant differences in the intercepts were also found between Macarella and S'Enclusa (Table IV-4).

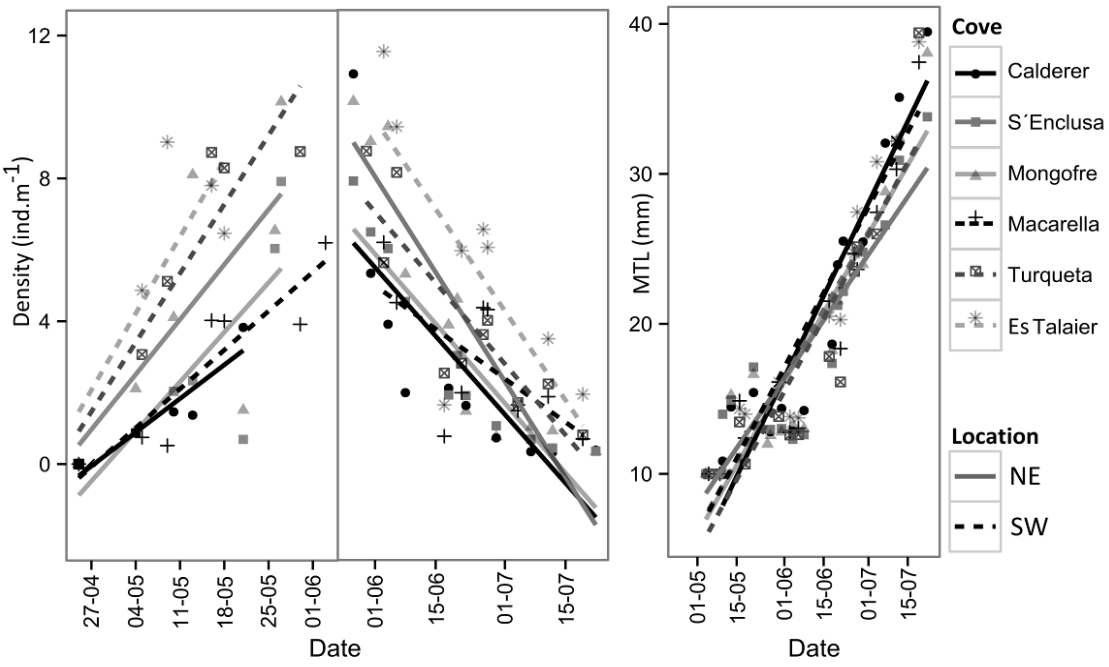

Fig. IV-5. Predicted relationship between ID (density increase, ind.day^{-1}.m^{-1}) and DD (density decrease, ind.day^{-1}.m^{-1}), and MTL (Mean Total Lenght, mm) of juvenile *Diplodus sargus* with time at each cove placed in the NE (northeast) and SW (southwest) locations.

Table IV-4. Results of the predicted relationship between increases and decreases in population density and Mean total length trends of *Diplodus sargus* with time at each cove, and results of the analyses of covariance (ANCOVA) comparing the increase and decrease in population rate (ind.day^{-1}.m^{-1}) and Mean total length trends among coves (ID, DD and MTL trends, respectively). a: intercept: b: slope; r2: coefficient of determination; Df: degrees of freedom; MS: mean squared; F: F- statistic, with its Degrees of freedom (DF) and its significance (P).

ID					
Lineal Regression	a	b	r2	F	P
Calderer	-2.475±3.237	0.331±0.149	0.497	4.949(1-3 DF)	0.113
S'Enclusa	0.311±2.291	0.220±0.102	0.381	4.686(1-5 DF)	0.083
Mongofre	-1.071± 1.570	0.199±0.070	0.543	8.132 (1-5 DF)	0.036
Macarella	-0.545± 0.773	0.156±0.031	0.800	25.01(1-5 DF)	0.040
Turqueta	0.640± 1.234	0.276±0.058	0.812	22.59(1-4 DF)	0.009
Es Talaier	1.039 ±1.636	0.317±0.077	0.761	16.87(1-4 DF)	0.015
ANCOVA	Df	MS	F	P	
Date	1	245.49	47.776	<0.001	
Cove	5	21.41	4.167	0.007	
Date *Cove	5	3.92	0.763	0.585	
Residuals	26	5.14			
DD					
Lineal Regression	a	b	r2	F	P
Calderer	13.269 ±2.405	-0.174 ± 0.041	0.606	17.9 (1-10 DF)	0.002
S'Enclusa	15.305 ±1.710	-0.191±0.028	0.816	45.39(1-9 DF)	<0.001
Mongofre	11.165 ±1.087	-0.139±0.018	0.8543	59.62(1-9 DF)	<0.001
Macarella	8.292 ±2.305	-0.087 ± 0.036	0.372	5.741 (1-7 DF)	0.048
Turqueta	12.441 ±1.727	-0.142 ± 0.028	0.731	25.39 (1-8 DF)	0.001
Es Talaier	3.593 ±0.541	-0.029 ± 0.009	0.519	10.71(1-8 DF)	0.011
ANCOVA	Df	MS	F	P	
Date	1	436.4	125.699	<0.001	
Cove	5	14.5	4.182	0.003	
Date *Cove	5	4.1	1.185	0.330	
Residuals	51	3.5			
MTL trends	a	b	r2	F	P
Linear Regression					
Calderer	1.681±2.153	0.388±0.041	0.866	91.54(1-13 DF)	<0.001
S´Enclusa	5.947±1.856	0.275±0.036	0.792	58.06(1-14 DF)	<0.001
Mongofre	3.680±1.968	0.328±0.038	0.829	73.59(1-14DF)	<0.001
Macarella	3.557±1.868	0.356±0.035	0.885	101.3(1-12DF)	<0.001
Turqueta	2.315±2.379	0.347±0.045	0.818	59.38(1-12DF)	<0.001
Es Talaier	4.029±1.910	0.325±0.036	0.860	80.66(1-12DF)	<0.001
ANCOVA	Df	MS	F	P	
Date	1	5136	451.916	<0.001	
Cove	5	6	0.538	0.747	
Date*Cove	5	11	0.965	0.444	
Total	77	11			
Post-hoc Tukey HDS test	ANCOVA ID			ANCOVA DD	
Macarella-Calderer	0.732			0.948	
Mongofre-Calderer	0.964			0.992	
S´Enclusa-Calderer	0.988			0.064	
Es Talaier-Calderer	0.276			0.003	
Turqueta-Calderer	0.776			1.000	
Mongofre-Macarella	0.987			0.723	
S´Enclusa-Macarella	0.262			0.012	
Es Talaier-Macarella	0.007			0.001	
Turqueta-Macarella	0.070			0.964	
S´Enclusa-Mongofre	0.622			0.232	
Es Talaier-Mongofre	0.033			0.018	
Turqueta-Mongofre	0.236			0.991	
Es Talaier-S´Enclusa	0.534			0.838	
Turqueta-S´Enclusa	0.971			0.078	
Turqueta-Es Talaier	0.940			0.005	

IV.3.2.2. Influence of physical forcing in juvenile dynamics

Influence of physical forcing in settlement and post-settlement dynamics of white seabream were summarised by two final GAM models describing fish MD and MTL. The final GAM model selected for MD was a model including miT, Swi, and Dwi without interactions with coves (Table IV-5). Water temperature was strongly correlated with Date and hence density GAM analysis revealed that the settlement peak coincided with intermediate values of miT, while density decreased hereafter as the warmer seasons advanced. More interestingly, the GAM analysis revealed that juvenile density decreased as wind speed increased and that winds blowing form the SE were also associated to lower density values (Table IV-5, Fig. IV-6).

Table IV-5. Final GAM best formulations selected, proportion of variance explained (%DE), adjusted R^2 ($Radj^2$), and genuine cross validation (GCV) of the best models for dynamics (mean density, MD); and total length mean trends (MTL). All the terms included in these models were statistically significant ($p < 0.1$); f_1,f_2 (…)f_8 are smooth functions estimated by the model by maximum likelihood, ε is the stochastic component. miT: minimum temperature, Swi: wind speed, Swi5: wind speed 5 days before census, Dwi: wind direction, and lD: logarithm of mean density (log ind. m^{-1}+1).

Model	Dependent variable	Formulation	%DE	$Radj^2$
Final GAM Mean density	MD	$D=cove+f_2(miT)+f_3(Swi)+f_4(Dwi)+\varepsilon$	87.1	0.637
Final GAM MTL	MTL	$MTL=cove+f_5(lD)+f_6(miT)+f_7(Swi)+f_8(Swi5)+\varepsilon$	97.9	0.84

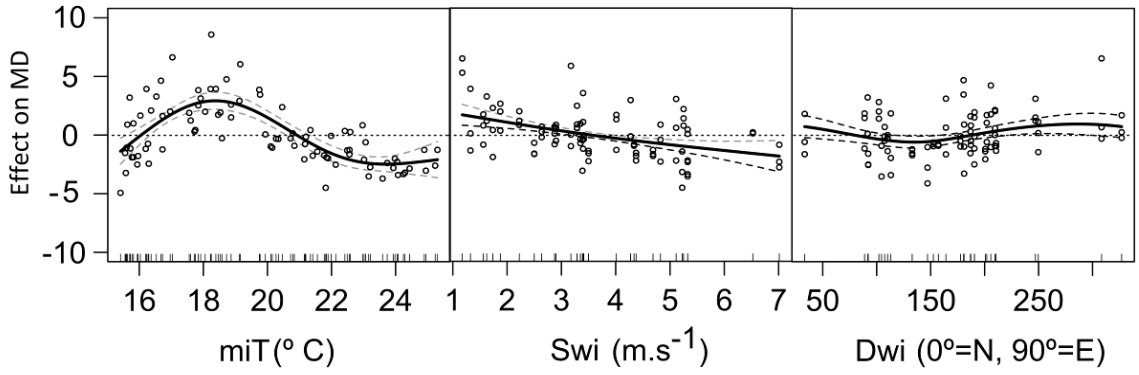

Fig. IV-6. Summary of the significant forcing factors found to affect the density of *Diplodus sargus*. Obtained from the best GAM MD (mean density) model, including: miT (minimum temperature, ºC, $p<0.001$), Swi (wind speed, $m.s^{-1}$, $p=0.001$) and Dwi (wind direction, 0°=North, 90°= Est, $p=0.029$). Fitted lines (solid line), 95% confidence intervals (areas between gray dotted line) and partial residuals (dots) are shown.

The final GAM model selected for MTL included lD, miT, Swi, Swi5 as additive effects without interactions with coves (Table IV-5). As expected, the lowest MTL corresponded to the highest juvenile density values recorded during settlement of early juveniles and MTL increased as temperature increased and the warm seasons progressed. More interestingly, high wind speed, either on the survey day or five days before, was associated to higher MTL values (Table IV-5, Fig. IV-7).

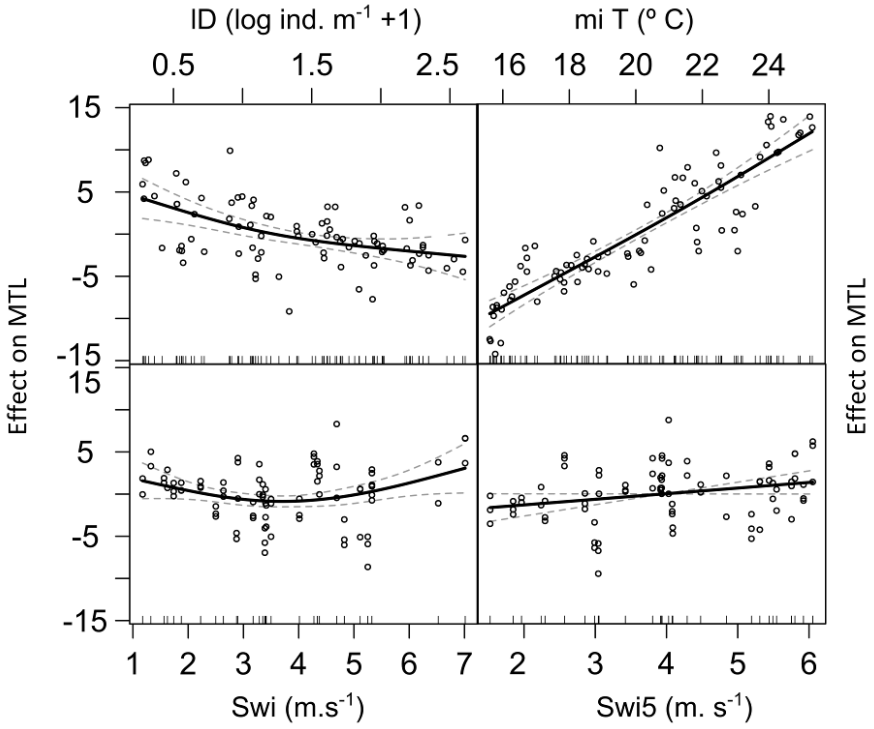

Fig. IV-7. Summary of the significant forcing factors found to affect *Diplodus sargus* MTL (Mean Total Lenght). Obtained from the best GAM MTL (mean total length) model, including: lD (logarithm of mean density, log ind. m^{-1} +1, p=0.004), miT (minimum temperature, ºC, p<0.001), Swi (wind speed, $m.s^{-1}$, p=0.028), and Swi5 (mean wind speed 5 days before census, $m.s^{-1}$, p=0.051).

IV.4. DISCUSSION

Processes driving settlement and post-settlement of white seabream around Minorca island seem to operate at island scale, as shown by the high synchrony observed in the dynamics of the juvenile population at coves which are tens of kilometres apart (~30 km), or on the same side of the island, much closer (i.e.: between ~500 m and 2 km apart). However, some variations in the different juvenile density population phases (arrival date, increase and decrease) were found. For instance, the first strong larval input was not detected or

was very slight at the NE coves (Calderer and Mongofre, respectively), where an apparent lag in settlement occurred.

Spatio-temporal variability in fish settlement and recruitment has already been reported elsewhere (e.g. Cowen, 1985; Doherty and Williams, 1988; Victor, 1986). The settlement peak densities shown in this study ranged between 6 ind.m^{-1} and 12 ind.m^{-1}, which are among the highest peak density values reported for white seabream in the Mediterranean (Table IV-6). All these studies were conducted on locations with suitable nursery habitats for white seabream, i.e.: shallow (<2 m depth) gently sloping coves with heterogeneous substrata of sand, pebbles and rocky bottoms (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). Consequently habitat-suitability should not be the reason explaining variations in peak densities among coves and locations. Rather, these differences could be the result of processes more related with larval processes, such as different distance from larval sources (spawning stocks), and/or differential larval dispersal and subsequent larval supply (Di Franco et al., 2012). In turn, these processes are influenced by a combination of explaining factors: i) behaviour of larvae (Pineda et al., 2010); ii) their swimming capabilities (Fisher, 2005; Fisher et al., 2000), iii) hydrodynamics processes such as waves and turbulent fluxes (Pineda et al., 2010); iv) positive stimulus such as biochemical (Gerlach et al., 2006) and physical stimulus (Montgomery et al., 2006; Simpson et al., 2005; Sponaugle and Cowen, 1996); v) biological interactions (e.g. predation, competition); vi) larval physiology (age, competency, energy reserves, growth) (Bergenius et al., 2002; Vigliola, 1998; Ware, 1975) and vii) habitat structure and topography (Cheminee et al., 2011; Félix-Hackradt et al., 2013b), which may also have a bearing on final settlement densities.

Table IV-6. Different *Diplodus sargus* maximum settlement population peaks reported in several areas of the Mediterranean (ind.m^{-1}). Locations: 1) Marseille (France); 2) Girona (Spain); 3) Banyuls (France); 4) Portofino (Italy); 5) Elba (Italy); 6) French Catalan coast (France); 7) Apulian Adriatic coast (Italy); 8) Cap Roux Fishery Reserve and adjacent areas in Saint-Raphaël (France); 9) Minorca island (Spain).

Location	PP (ind.m^{-1})	Year	References
1	16	1993-1995	(Vigliola et al., 1998)
2	7	1993-1995	(Vigliola et al., 1998)
3	>2	1994-1995	(Vigliola et al., 1998)
4	4	1994-1995	(Vigliola et al., 1998)
5	>3	1994-1995	(Vigliola et al., 1998)
6	>4	2005-2007	(Pastor et al., 2013)
7	4	2009-2010	(Di Franco et al., 2013)
8	>2	2011	(Arceo et al., 2012)
9	12	2012	This chapter
9	>5	2013	Chapter V

Such explaining factors are notably supposed to shape the initial larval input in nurseries (Raventos and Macpherson, 2005; Vigliola et al., 1998). Ultimately, explaining factors such as habitat structure (Anderson and Millar, 2004; García-Charton et al., 2004) may as well shape behavior at settlement and post-settlement survivorship (Bell and Westoby, 1986b; Thiriet et al., 2014; Tupper and Boutilier, 1997).

In our case, all studied coves were in a distance range smaller than the larval dispersal range reported for the white seabream (Di Franco et al., 2012). Thus, the very high density reported for Es Talaier, situated in the SW location, may be due to differential larval supply related to its different seascapes attributes, e.g. in terms of cove shape and microhabitat heterogeneity, providing post-settlers more refuges and hence, higher survival. Indeed, Talaier had a more heterogeneous bottom per surface than the remaining coves. Differences in habitat structure may determine different mortality-growth processes generating site-specific differences between coves (Cheminee et al., 2011; Félix-Hackradt et al., 2013b; García-Charton et al., 2004; Macpherson et al., 1997; Planes et al., 1998).

Furthermore, larval supply appears to be strongly influenced by local winds and currents (Félix-Hackradt et al., 2013b) and this was also true for white seabrams in Minorca. Our results showed that stronger winds were associated with lower juvenile densities and, more precisely, that strong SE winds were unfavourable for settlement in the NE area. The impact of the rough hydrodynamic event was stronger on the smallest fishes in all coves.

As a consequence, the increase in population density recorded since the onset of settlement was truncated and a general bimodal density pattern emerged after the rough hydrodynamic event. This bimodal density pattern could be detected throughout the post-settlement period as fish grew but it is not clear to what extent this temporal interruption of larval arrival may influence recruits and the future adult population structure.

Furthermore, the variation in density observed during the decreasing population phase found in the SW coves could be related with a higher mortality inside nurseries situated windward due to a major effect of the disturbance generated by the rough hydrodynamic event. Finally, higher mean TL were associated to higher wind speeds. It could be that smaller individuals were trying to avoid the disturbance generated by the high hydrodynamism caused by the wind, by moving a few meters deeper than their habitual depth range (Cheminee et al., 2011). Additionally, higher differences in decreasing densities were detected among NE coves probably related to a temporary interruption of the larval arrival because the downwind impeded or even pulled out larvae from the coast. Consequently, the final recruitment level, which was lower in the NE location, may reflect this larval input interruption and a higher larval supply at SW coves due to weather conditions. Thus, although no real differences between population increase and decrease rates were found between SW and NE coves, the rough hydrodynamic event of May, had different consequences for those coves situated windward (SW coves) or leeward (NE coves).

The co-occurrence of both larval release and dispersal, with specific climatic conditions may strongly shape the settlement success and subsequent recruitment (match-mismatch hypothesis; Cushing, 1969). These results and the interpretation are in agreement with Vigliola (1998), which argued that winds regimes regulate white seabream settlement in Marseilles Bay (France), and that winds from sea to coast favoured settlement. Furthermore, Raventos & Macpherson (2005) found that calm weather also favoured settlement for another necto-benthic species with pelagic larvae (*Symphodus* spp.) in Spanish Catalan coast.

In spite of the different values in settlement peaks found at the various coves in Minorca, the Recruitment Level (i.e.: the remaining juveniles) was very low in all cases. In our study, 87 to ~97 % of the juveniles died after 50-60 days from settlement peak, indicating high mortalities but with similar values as in other Mediterranean regions. For example,

Arceo et al (2012) found mortalities of up to 60 to ~ 99 %, after 50-60 days from the settlement peak in the Cap Roux Fishery Reserve and adjacent areas in Saint-Raphaël (France) in 2011. Similarly, Macpherson et al (1997) found mortalities from 50 to ~99%, after 50-60 days from the settlement peak in Gerona (Spain) and Marseille (France) in 1994-1995.

The importance of recruitment in front of other demographic processes determining adult local population densities is not clear (Caley et al., 1996; Holm, 1990) and only a few studies have simultaneously considered multiple life stages across multiple spatial scales. For instance, Di Franco et al. (2013), found no significant relationships between the density of adults, settlers, recruits and young of the year of white seabream, and attributed it to a possible decoupling in space between the sequential life history stages of fish caused by dispersal processes. Conversely, other studies found a significant relationship between the density of settlers or late juveniles and the recruitment level of *Diplodus* spp. (Planes et al 1998, Félix-Hackradt et al. 2013a). In any case, although prediction of adult population sizes is difficult based solely on juvenile stock data, they may determine in some way the availability of new individuals and the final replenishment of populations (Caley et al., 1996). In the case of Minorca island, white seabream adult densities are very low compared with those in other Mediterranean regions (Cardona et al., 2007a; Coll et al., 2012; Guidetti and Sala, 2007; Sala et al., 2012), in spite of the high settlement values reported here. Cardona et al. (2007) hypothesized that adult density of white seabram in Minorca was low because of the oligotrophy of the coastal waters around the island, but the results reported here indicate that post-settlement processes at nursery habitats are more likely the limiting factor. Nevertheless, further studies are necessary to assess the temporal and spatial relationships between juvenile and adult white seabream.

IV.5. CONCLUSIONS

Similar dynamics were globally reported at the scale of the island for the settlement and recruitment of white seabreams, although differences in juvenile density were observed between some coves, suggesting the importance of site-specific conditions for their nursery value. The intensity of settlement peaks was particularly variable among coves, but juvenile density at the end of settlement period (i.e. recruitment level) was globally low in all coves, suggesting that density-dependent mortality levelled initial differences in settlement. Furthermore, a rough hydrodynamic event observed during the central settlement period, with moderate winds from the SE, dramatically affected larval supply in the NE location, resulting in lower recruitment level. Thus, it is plausible that areas with frequent rough hydrodynamic events display lower densities of white seabreams. Future research on the influence of environmental variables on fish life history should properly assess the related spatial and temporal variability at multiple scales and at multiple life phases in order to better account for their possible influences on final adult population replenishment.

Chapter V. Influence of landscape attributes at different spatial scales on the density of juveniles *Diplodus sargus*

Photo V-1. *Diplodus sargus* juveniles: 15-20 mm Total Length. Minorca island, depth= 1 meter, May 2013. Photo: Amalia Cuadros.

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Chapter V. Influence of landscape attributes at different spatial scales on the density of juveniles *Diplodus sargus*

V.1. INTRODUCTION

V.1.1. Context of this study

Chapters II and III studied the influence of seascape attributes, at various spatio-temporal scales on the assemblages of juvenile littoral fishes. Chapter IV focused on the effect of weather conditions, mainly winds, on the density of the earlier stages of *Diplodus sargus* and suggested a relationship between seascape attributes and the effect of winds: a given coastal orientation shaped the off-shore direction of dominant winds, influencing negatively the settlement and post-settlement dynamics. Here in Chapter V, we aimed to gain a deeper insight on the influence of seascape attributes on the settlement and post-settlement dynamics of this species, particularly broad scale location, site-specific cove exposure and within site variability of microhabitat types.

Most marine species have a pelagic stage which is potentially dispersive (eggs, larvae) (Christie et al., 2010; Di Franco et al., 2012). Afterwards, an ontogenetic transition from the planktonic to the benthic habitats occurs in most benthonic species in a process called ‘settlement’(Thresher et al., 1989). The initial density of individuals available for settlement is shaped by the number of planktonic larvae available near benthic habitat resulting of their dispersion, i.e. the larval supply (Asplin et al., 1999; Peck et al., 2012; Pineda et al., 2010; Victor, 1986; Watson and Munro, 2004). Settlement success is measured by the maximum number or “peak” of recently settled individuals or “settlers” (Levin, 1994; Macpherson et al., 1997; Macpherson and Zika, 1999). Hereafter adult populations are replenished with the “late juveniles” whom survived after settlement and developed in juvenile habitats, joining adult populations in a process called “recruitment”. “Recruits” are the juveniles already present in adult habitats (Thiriet, 2014). Frequently, the potential recruitment is measured by the number of late juveniles remaining after an

arbitrary period of time following the main settlement event (i.e. “recruitment level”) (Levin, 1994; Macpherson et al., 1997; Macpherson and Zika, 1999).

Consequently, various processes act at nested spatial scales shaping the recruitment level of benthic species: dispersal until larval supply in benthic habitats, at broad scale, and settlement and post-settlement processes in benthic habitats, at lower scale.

Dispersal and subsequent larval supply to juvenile habitats are highly influenced by seascape connectivity, which in parallelism to landscape connectivity (Brooks, 2003) may be defined as the degree to which the seascape facilitates or impedes individuals’ movement among resource patches (Cheminée et al., 2014; Taylor et al., 1993). According to Calabrese and Fagan (2004), connectivity has two components: the functional connectivity (dispersal abilities between populations of individuals and species) and structural connectivity (the physical connection of populations). Regarding functional connectivity, biological processes have been highlighted as important for larval dispersal and subsequent larval supply. For example, spawners tends to take advantage of specific periods and areas of high productivity, special predator-prey relationships, and conditions affecting transport of spawning products (match/mismatch hypothesis) (Cushing, 1974, 1969; Hjort, 1914; Norcross and Shaw, 1984; Vigliola, 1998; Vigliola et al., 1998). In the same sense, specific planktonic larval duration, pelagic *versus* demersal egg (Berumen et al., 2012; Bradbury et al., 2008), larval swimming capacities (Bellwood and Fisher, 2001; Stobutzki and Bellwood, 1997), and larval habitat selection among settlement areas (Bell and Westoby, 1986a; Gerlach et al., 2006; Leis and Carson-Ewart, 1998; Montgomery et al., 2006; Simpson et al., 2005; Stobutzki and Bellwood, 1997) regulate functional connectivity. Structural connectivity, maybe mainly determined by currents, weather conditions, and seabed topography and coast morphology (Bradbury et al., 2008; Cowen and Sponaugle, 2009; Gilg and Hilbish, 2003).

Once larvae arrive near juvenile habitats, juvenile microhabitat availability (subsets of biotic and abiotic habitat components (Chapman, 1995)) is very important to accomplish settlement (Beck et al., 2001; Cheminée et al., 2014; Nagelkerken et al., 2015; Parsons et al., 2014). Often, fish juveniles have strict taxa specific microhabitat requirements for settlement (Bussotti and Guidetti, 2010; Cheminée et al., 2013; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Macpherson and Zika, 1999, 1999), that

may change as early juveniles grow (Dahlgren and Eggleston, 2000; Macpherson, 1998). Finally, Post-settlement processes (juvenile growth and survival in benthic habitats until they acquire capacity to move, if required, towards adult habitats) depend on the habitat quality, i.e., the trade-off between food and shelter availability (Beck et al., 2001; Cheminée et al., 2013; Gibson, 1994; Hobbs et al., 2006; Thiriet et al., 2014).

Since seascape attributes at different scales plays an important role in larval dispersion, larval supply, settlement and post-settlement, they may have an impact on the final late juvenile production. However, the relative importance of settlement and post-settlement processes on determining the amount of late juveniles available for recruitment is still poorly known (Félix-Hackradt et al., 2013a; Raventos, 2009; Vigliola et al., 1998); furthermore the seascape scale at which they operate is poorly known.

Here we propose two extreme scenarios related to seascape. In one hand, variability of final late juvenile production among sites may depend mainly upon settlement processes (i.e. initial density variability) which in turn will be mainly shaped by larval supply. Larval supply variability may be influenced by landscape at larger scales. This initial density variability may persist in time because of a negligible effect of post-settlement processes. On the other hand, final variability of late juveniles could be shaped mainly by post-settlement processes (e.g. growth and survival of juveniles in juvenile habitats) influenced in turn by habitat local features such as microhabitats characteristics.

To quantify the relative importance of settlement and post-settlement processes in the recruitment success of Mediterranean reef fishes, we selected the white seabream, *Diplodus sargus* (Linnaeus, 1758). As mentioned in Chapter IV, *D. sargus* is particularly relevant. It is an abundant species (Froese and Pauly, 2011), with a commercial and recreational interest (Lloret et al., 2008) and with a functional role in Mediterranean rocky communities (Giakoumi et al., 2012; Guidetti, 2006). Populations of *D. sargus* have been suggested to be recruitment limited in some areas (Cardona et al., 2007b) and different authors reported high spatial variability on its settlement rates and recruitment levels (Arceo et al., 2012; Cheminee et al., 2011; Macpherson et al., 1997; Vigliola et al., 1998).

V.1.2. Objectives of Chapter V

The objective of the present work was to quantify and compare *D. sargus* settlement and post-settlement densities under the influence of contrasted seascape attributes, at different spatial scales in Minorca island (NW Mediterranean; it aimed to better understand the causes of the spatial variability of juvenile densities reported for such species. Firstly, we tested the effect of coastal location by comparing coves facing contrasted hydrographic regimes (north *vs.* south coast of the island) and hence likely to experience differences in larval supply which may be reflected in settlement success and recruitment level. Secondly, and crossed with location, we tested the effect of cove configuration in terms of exposure level, which may also have an influence on larval supply and consequently in settlement success and recruitment level. Furthermore, within each cove we measured the importance of post-settlement processes (growth or survival), which may determine recruitment levels. Finally, within each cove we tested the effect of microhabitats features on juvenile densities.

V.2. MATERIAL AND METHODS

V.2.1. Studied area

The study was conducted along the coast of Minorca island, at the center of the north-western Mediterranean (Fig. V-1). The island spans about 50 km from west to east and about 20 km from north to south and its coastline measures 441 km (Sales, 2007). The island is an ideal study locality since its coasts presents contrasted exposure and orientation conditions. Indeed, the island coast can be divided into two differentiated regions (north and south, see Llompart et al.(1979)) with differentiated wind influences and facing different water masses: those from the Lion Gyre affect the north shore (López-Jurado et al., 2008) and those from the Algerian Basin affect the south shore (Bethoux, 1980; Millot, 1999; Pinardi and Masetti, 2000). Furthermore all along the island coast, the shoreline displays series of coves more or less enclosed.

Based on a preliminary study (Chapter I and Chapter IV), sites were selected in the island according to the availability of suitable nursery habitats for *D. sargus*: shallow (less than 2 m deep), gently sloping substrates of gravel, pebbles, or boulders (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Macpherson, 1998) (Photo V-II).

V.2.2. Sampling design

The study was conducted in twelve coves selected according to crossed factors: location (two levels: north and south) and cove configuration in terms of exposure (two levels: exposed and sheltered) (see Fig. V-1). To define the two exposure levels we adapted Miller's index of exposure (1985) to Minorca coves: sheltered and exposed coves were respectively without and with line of sight to the open ocean (Fig. V-1). Our quantitative exposure categories were in agreement with categories proposed by Balaguer et al (2007) and Canellas Moragues (2010).

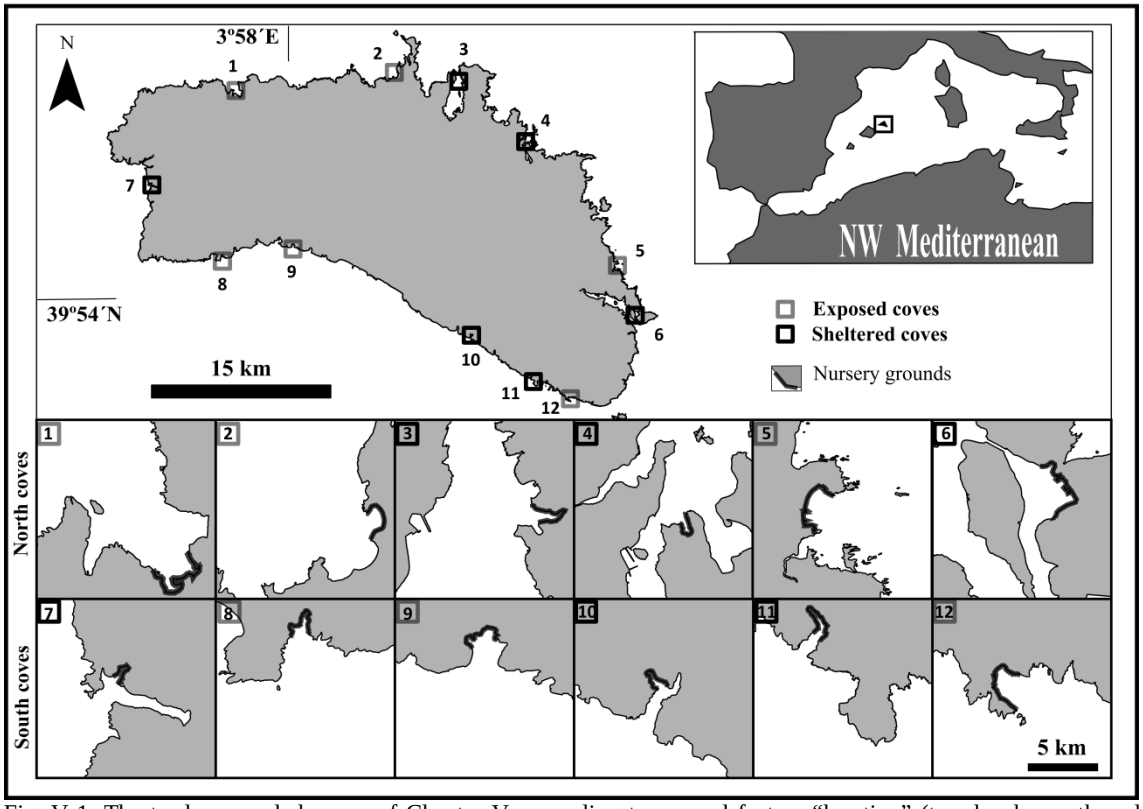

Fig. V-1. The twelve sampled coves of Chapter V, according to crossed factors "location" (two levels: north and south) and "exposure" (two levels: exposed (gray squares) and sheltered (black squares)). 1= "Estancats" (40º2´46.65" N, 3º55´19.47" E), 2=: "Rotja" (40º3´44.06" N, 4º4´37.19" E), 3= "Cabra Salada" (40º3´18.31" N, 4º8´30.76" E), 4= "S´Esmolador" (40º0´29.09" N, 4º0´29.09" E), 5= "Sa Mesquida" (39º54´55.43" N, 4º17´15.10" E), 6= "Taulera" (39º52´40.92" N, 4º18´34.44" E), 7= "Sa Caleta" (39º58´52.38" N, 3º50´2.80" E), 8= "Es Talaier" (39º55´33.43" N, 3º54´7.71" E), 9= "Mitjana" (39º56´2.33" N, 3º58´19.68" E), 10= "Cales Coves" (39º51´51.13" N, 4º8´41.37" E), 11= "Biniparratx" (39º 49´59.21" N, 4º12´11.47" E), 12= "Binibeca" (39º48´57.00" N, 4º14´23.87" E).

We additionally differentiated three microhabitat types inside each cove (Macpherson, 1998) (Fig. V-2): "beach area" (BA) usually characterized by a dominance of sandy sediments and a depth of 0-50 cm; "mixed areas" (MA) with heterogeneous substratum of rocks, boulders, pebbles and sand ranging 50-100 cm in depth (Photo V-II); and "rocky areas" (RA) with a dominance of rocky substratum ranging 50-300 cm in depth. Typically, beach areas are in the innermost part of the cove, rocky areas close to the mouth and mixed areas in between (Fig. V-2).

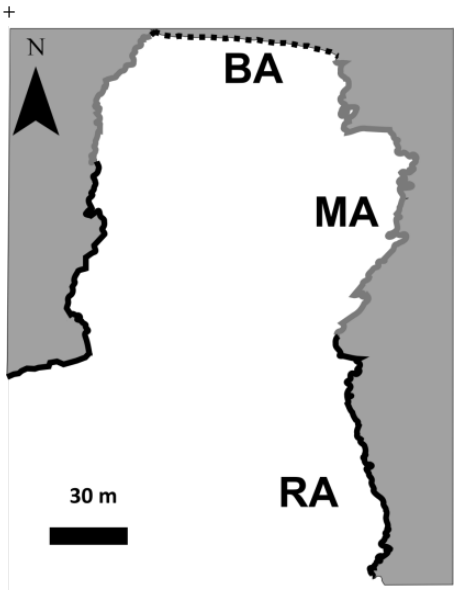

Fig. V-2. Example of microhabitats sampled among each nursery cove (here: Est Talaier cove). Line type corresponds to microhabitat type: “beach area” (BA, thick dotted line); “mixed area” (MA, continuous gray line); “rocky area” (RA, continuous black line).

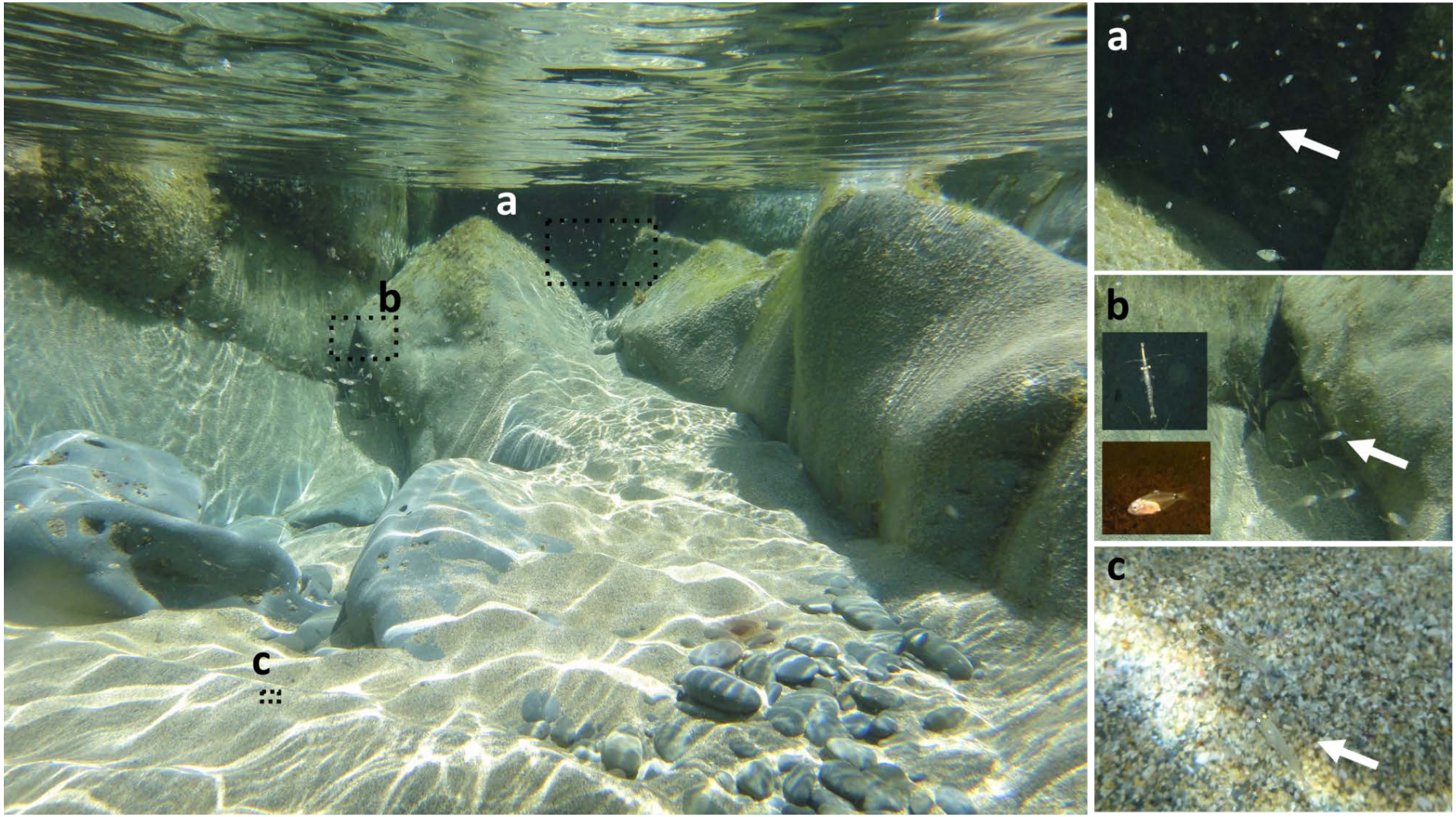

Photo V-2. Nursery habitat of *Diplodus sargus*. Microhabitat type "Mixed areas" (MA) with heterogeneous substratum of boulders, pebbles and sand ranging 50-100 cm in depth. Foreground spans around 1.5 m wide. Visible juveniles in this shot are *D. sargus* settlers (a,b,c, 10-15 mm Total Length, marked with arrows), one *D. vulgaris* (a, 20 mm TL); Juveniles are found in mixed shoals with the invertebrate Mysidacea (b) (Minorca island, depth= 0.5-1 meter, April 2012). Photos: Amalia Cuadros.

V.2.3. Data collection

Sampling was carried out from 17 th May to 18 th July, in 2013, i.e during the known *D. sargus* settlement period (Harmelin-Vivien et al., 1995). A total of 144 surveys were carried out (Table V-1). We sampled all coves at three different times, every two (or three) weeks. Additionally, exposed coves (which displayed higher juvenile densities, see results) were sampled weekly, when weather permitted, for the analysis of the microhabitat effect. Sampling days were randomly chosen among days presenting good weather conditions, since weather is known to affect density estimations (Harmelin-Vivien et al., 1985). Surveys were conducted between 7 am and 11 am, avoiding the time slots of higher frequentation by bathers (Juaneda and Roig, 2002; Munar and Xavier, 2003).

Sampling was carried out snorkelling along pre-defined transects running parallel to the shoreline (50 meters mean length). Underwater Visual Census (UVC) were performed according to previously established methodologies and covering depth until 3 m (Cheminee et al., 2011; Harmelin-Vivien et al., 1985). The beginning and the end of each transect were referred to some physical features of the topography of the coastline, to ensure accurate repeatability along the time. Each time, the entire cove was completely sampled by the same diver snorkelling. The juveniles in each cove were counted and their total length (TL) was estimated with the help of fish silhouettes of different sizes pictured on the slate (5 mm TL size-classes from 10-15 mm to 80-85 mm TL) (Cheminee et al., 2011; Cheminée et al., 2013; Pastor et al., 2013; Vigliola et al., 1998). The precision of this size estimating method was estimated about ± 3.5 mm for *Diplodus* species (Macpherson, 1998). For the analyses, juvenile fish densities were standardised to one linear meter of shoreline (ind.m^{-1}) (Cheminee et al., 2011; Harmelin-Vivien et al., 1985).

Table V-1. *Diplodus sargus* census of Chapter V. Number of sampling days (NSD), transects (T), total number (TN) of white seabream juveniles censed during the study period, maximum number of juvenile censed in one day (MNJ) and size ranges (total length, TL) recorded in each cove. The location (north, south), exposure (exposed, sheltered), shoreline length (SL), and % of each habitat type (BA: beach areas, MA: mixed areas, RA: rocky areas) for each cove are also indicated.

Cove	Location	Exposure	SL (m)	BA (%)	MA (%)	RA (%)	NSD (nº)	T (nº)	TN (nº)	MNJ (nº)	TL (mm)
Estancats	North	Exposed	910.68	23.3	17.8	58.9	7	70	6 115	1 114	10-60
Rotja	North	Exposed	365.58	0	43.3	56.7	8	48	5 068	937	10-70
Sa Mesquida	North	Exposed	717.41	27.8	57.0	15.2	8	72	5 982	1 283	10-60
Cabra Salada	North	Sheltered	315.38	26.3	22.4	51.3	3	24	43	28	15-70
S´Esmolador	North	Sheltered	365.76	28.4	21.3	50.4	3	21	19	15	15-60
Taulera	North	Sheltered	938.02	9.0	32.2	58.9	3	33	102	41	10-60
Es Talaier	South	Exposed	408.69	8.6	46.0	45.4	7	27	15 385	3 683	10-60
Mitjana	South	Exposed	475.4	29.5	45.5	25.0	7	77	10 076	1 987	10-60
Binibeca	South	Exposed	495.18	18.7	19.8	61.5	7	63	4 080	903	10-60
Sa Caleta	South	Sheltered	402.33	5.7	33.5	45.1	3	21	793	389	10-60
Cales coves	South	Sheltered	312.23	26.3	22.4	51.3	3	18	100	58	10-60
Biniparratx	South	Sheltered	516.45	5.1	22.9	72.0	3	27	89	49	15-60

V.2.4. Statistical analyses

In order to study juvenile population dynamics according to the three seascape attributes (i.e. location, exposure, and microhabitat type, thereafter named as treatments), five response variables were analyzed: 1) multivariate density temporal patterns; 2) univariate density at each of the three simultaneous surveys; 3) univariate daily mean total length; 3) univariate daily mean total density; and 4) univariate mean juvenile density by size-class.

In order to test the crossed influence of location and exposure, fish large enough to immigrate or emigrate were excluded (i.e. for *D. sargus*, >40 mm TL; Vigliola (1998)) and only density data corresponding to the three surveys conducted simultaneous at all coves were considered (hereafter referred as “first”, “second” and “third” surveys). First, multivariate juvenile density patterns across the three surveys were compared by means of a PERMutational multivariate ANalysis Of VAriance (PERMANOVA) (Anderson, 2001) Type III, based on the Binomial deviance (scaled) measure of distance (Anderson and Gorley, 2008). Crossed terms included in the model were: location as a fixed factor (two levels: north vs. south) and exposure as a fixed factor (two levels: exposed vs. sheltered). Furthermore, when interactions of factors were significant we applied pair-wise comparison tests. Secondly, for each mentioned survey, a univarite PERMANOVA Type III, using Euclidean distances, was applied in order to compare density between treatments levels (location, exposure). First and second surveys corresponded respectively to census

from days 2/06 to 8/06 and days 20/06-23/06. The first survey was considered as a proxy of settlement peak (i.e. 10-15 mm TL fish peak density) since when sampling started, juveniles of 10-15 mm were already present (Cheminee et al., 2011). Third survey corresponded to days 16/07-18/07 and it was considered as a measure of the recruitment level (Macpherson and Zika, 1999). For these permutational analyses and to model our various response variables as a function of the treatments, P-values were obtained by 999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<200). Terms were pooled as suggested by Anderson et al. (2008).

Since sheltered coves supported very low fish (see results), only exposed coves were considered for subsequent analyses. Daily juvenile mean total length (MTL) (mm) and daily total density ($ind \cdot m^{-1}$) of each cove were used in Least squared regression analyses to calculate regression slopes ("b") and obtain respectively juvenile growth rates ($mm\ day^{-1}$) and density decrease rates ($ind \cdot m^{-1} \cdot day^{-1}$) for each cove. These rates were used to describe the post-settlement population dynamics. Regressions were calculated using on one hand the daily MTL of all the juveniles present at each cove, from the first to the last sampling day ; and on the other hand density decrease rates were calculated considering the density of individuals from the first to the last day of sampling and excluding fish with possible immigration or emigration capabilities (i.e. for *D. sargus*, >40 mm TL, Vigliola (1998)). Analysis of covariance (ANCOVA) was used to test the effect of cove (included as a categorical factor in the model) on MTLs and densities, considered as dependent variables, while controlling for the effect of time, considered as a continuous co-variable. Tukey HSD post-hoc comparisons between coves were performed for MTL and density when appropriate.

Finally, ontogenetic changes in habitat use were assessed by comparing the density of juveniles of different size-classes occurring at the three microhabitats within each cove. All the juveniles observed at the nurseries were considered and they were split in five size-classes: (in mm TL): [10-25), [25-40), [40-55), [55-70). The [70-85) mm TL size class was not considered for further analyses due to the low number of fish (n<10). Each size class was analysed separately in a univariate PERMANOVA Type III, using Euclidean distances. In the model, factor microhabitat had three levels (BA, MA and RA) and was fixed; and factor cove had six levels (Estancats, Rotja, Sa Mesquida, Es Talaier, Mitjana,

Binibeca) and was fixed. Terms were pooled as suggested by Anderson et al. (2008). P-values were obtained by 999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<200).

Since ecological data are by nature highly variable, in this work terms were considered significant for P-values < 0.1. All data treatment and analyses were performed using the R 2.15.0 statistical software (R_Development_Core_Team, 2013) and PERMANOVA+ add on package for PRIMER software (Anderson and Gorley, 2008; Clarke and Gorley, 2006).

V.3. RESULTS

V.3.1. Effect of location and exposure on juvenile density temporal patterns

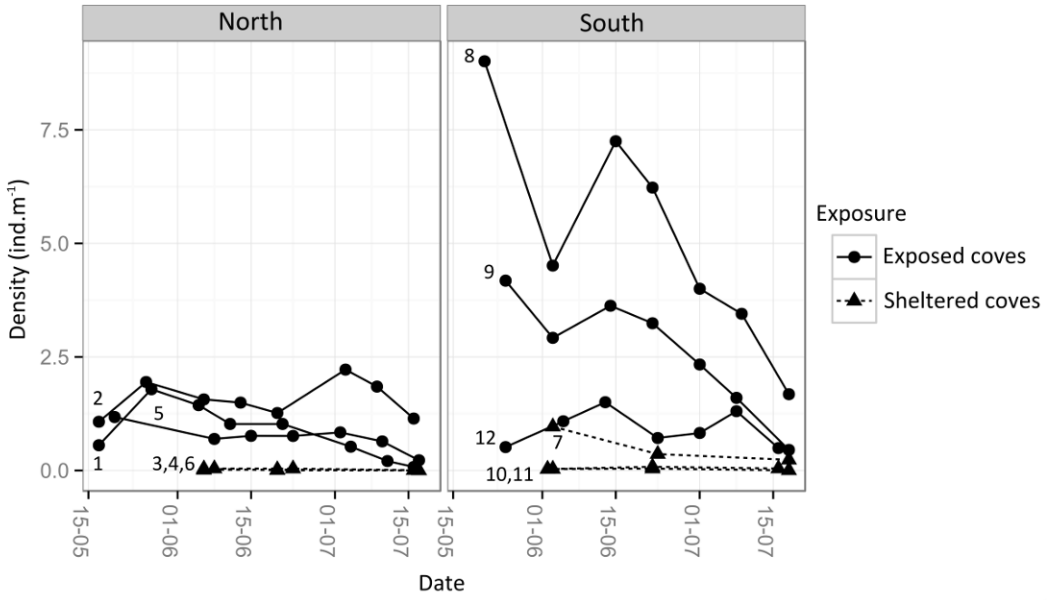

Fig. V-3. *Diplodus sargus* juvenile density (ind.m^{-1}) in each cove (coves 1 to 12) through time, according to location (north vs south) and exposure (exposed vs sheltered). Coves: 1= "Estancats", 2=: "Rotja", 3= "Cabra Salada", 4= "S´Esmolador", 5= "Sa Mesquida", 6= "Taulera", 7= "Sa Caleta", 8= "Es Talaier", 9= "Mitjana", 10= "Cales Coves", 11= "Biniparratx", 12= "Binibeca".

Densities trends were different between exposed and sheltered coves, whatever the location, although the magnitude of the difference was greater in the south coves, which resulted in a significant interaction term (PERMANOVA, Table V-2). As a general pattern, a decreasing density trend was observed in the all exposed coves, from the beginning to the end of the sampling period (Fig. V-3). Conversely density remained close to zero ind.m^{-1} through the whole sampling period in the sheltered coves (Table V-3).

Table V-2. PERMANOVA table of results: effect of location and exposure on multivariate juvenile *Diplodus sargus* density time series (ind.m^{-1}). Significance: ·P≤0.1 ; * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

Source of variation	Df	MS	Pseudo-F	P(perm)
Location (lo)	1	0.58	2.03	0.131
Exposure (ex)	1	6.26	21.94	**0.003****
lo x ex	1	0.91	3.18	**0.052**·
Residuals	8	0.29		
Total	11			

Table V-3. Density of *Diplodus sargus* juveniles obtained in each cove at the three surveys for all coves (ind.m^{-1}): first survey (proxy of settlement peak), second survey, and third survey (proxy of recruitment level).

Location	Exposure	Cove	First survey (ind.m^{-1})	Second survey (ind.m^{-1})	Third survey (ind.m^{-1})
North	Exposed	Estancats	0.694	0.760	0.224
		Rotja	1.565	1.264	1.143
		Sa Mesquida	1.437	1.023	0.077
	Sheltered	Cabra Salada	0.013	0.019	0.000
		S´Esmolador	0.038	0.005	0.000
		Taulera	0.041	0.039	0.005
South	Exposed	Es Talaier	4.512	6.230	1.679
		Mitjana	2.920	3.241	0.452
		Binibeca	1.082	0.715	0.493
	Sheltered	Sa Caleta	0.964	0.360	0.234
		Cabra Salada	0.032	0.080	0.042
		Biniparratx	0.031	0.041	0.002

In every survey, density varied according to exposure and not according to location (PERMANOVA, Table V-4) and juveniles were systematically more abundant in exposed coves (Table V-3, Fig. V-4).

Table V-4. PERMANOVA table of results: location and exposure effect on univariate juvenile *Diplodus sargus* density of the three simultaneous surveys at all the coves (ind.m^{-1}); the first survey is a proxy of the settlement peak and third survey a proxy of the recruitment level. Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

First survey (proxy of settlement peak)

Source of variation	Df	MS	Pseudo-F	P(perm)
Location (lo)	1	2.76	3.19	0.105
Exposure (ex)	1	10.25	11.86	**0.009****
Lo x ex	1	1.26	1.45	0.292
Residuals	8	0.86		
Total	11			

Second survey

Source of variation	Df	MS	Pseudo-F	P(perm)
Location (lo)	1	4.76	2.47	0.151
Exposure (ex)	1	13.42	6.96	**0.019***
lo x ex	1	3.77	1.95	0.184
Residuals	8	1.93		
Total	11			

Third survey (proxy of recruitment level)

Source of variation	Df	MS	Pseudo-F	P(perm)
Location (lo)	1	0.18	0.84	0.384
Exposure (ex)	1	1.19	5.72	**0.039***
lo x ex	1	6.86.10-2	0.33	0.576
Residuals	8	0.21		
Total	11			

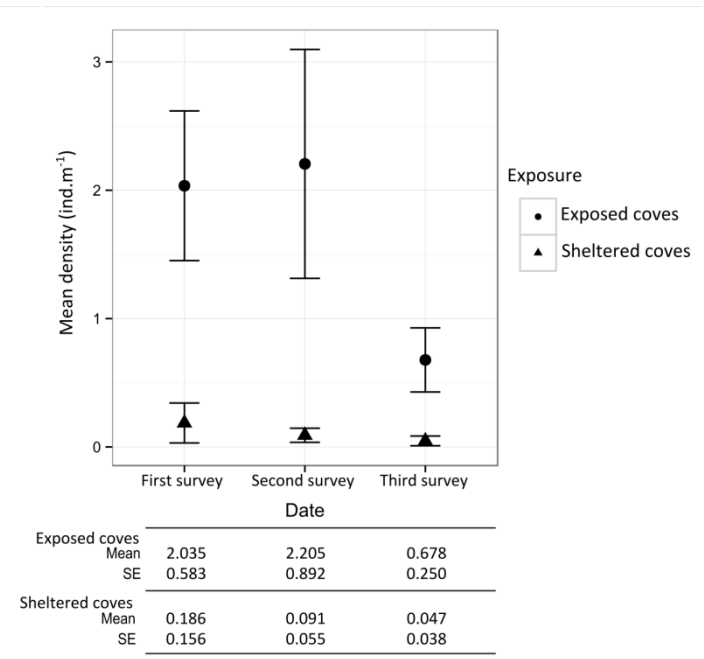

Fig. V-4. *Diplodus sargus* mean density (ind.m^{-1}) in each exposure level (exposed vs. sheltered coves) the three sampled dates for all coves: first survey was employed as a proxy of settlement peak, and third survey was considered a proxy of recruitment level. Mean and standard error (SE) values are given.

V.3.2. Post-settlement dynamics in exposed coves

V.3.2.1. Growth rates

For exposed coves, MTLs changed through time similarly in all coves (ANCOVA, Table V-5 and Fig. V-5) and corresponding growth rates (b) ranged from 0.375±0.043 mm.day^{-1} (in Mitjana) to 0.486±0.054 mm.day^{-1} (in Binibeca) (Table V-5).

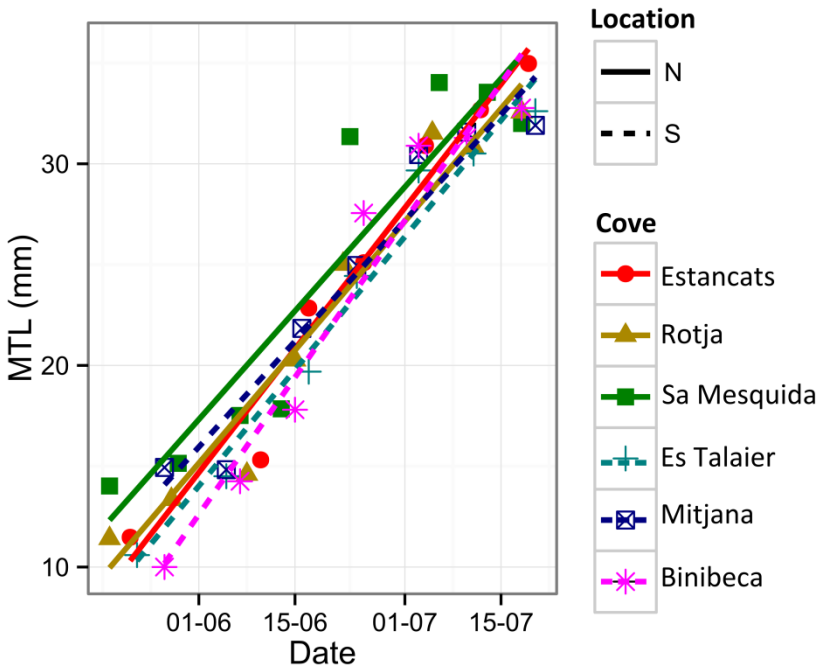

Fig. V-5. Observed data and predicted relationship of MTL (Mean Total Length, mm) of *Diplodus sargus* with time in each cove. Observed data=dots; predicted relationship =lines.

Table V-5. Results of the predicted relationship between Mean Total Lenghts (MTLs, mm) of juvenile *Diplodus sargus* with time in each cove and results of the analysis of covariance (ANCOVA) comparing the MTLs (mm) according to time and coves (interaction cove-day was removed because not significant). a: intercept: b: slope; r^2: correlation coefficient; Df: degrees of freedom; MS: mean squared; F: F statistic with its DF(Degree of freedom); and its significance ($\cdot$ $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$).

Exposure	Location	Lineal Regression	a	b	r^2	F	P
Exposed	North	Estancats	8.557±1.576	0.438±0.038	0.956	131.9 (1-5 DF)	**<0.001*** **
		Rotja	9.558±1.387	0.400±0.037	0.944	119.4 (1-6 DF)	**<0.001*** **
		Sa Mesquida	11.938± 2.408	0.384±0.063	0.839	37.45 (1-6 DF)	**<0.001*** **
	South	Es Talaier	8.248± 1.258	0.412±0.031	0.967	178.1 (1-5 DF)	**<0.001*** **
		Mitjana	10.709 ±1.763	0.375±0.043	0.924	74.26 (1-5 DF)	**<0.001*** **
		Binibeca	5.802± 2.163	0.486±0.054	0.931	81.94 (1-5 DF)	**<0.001*** **
ANCOVA			Df	MS	F	P	
Date			1	2645.8	483.31	<0.001***	
Cove			5	7.3	1.34	0.297	
Residuals			37	5.5			

V.3.2.2. Density decrease rates

For exposed coves, south coves "Talaier" and "Mitjana" presented significantly different density trends than the others, with higher decrease rates (b) (ANCOVA, Table V-6,Table V-7, and Fig. V-6).

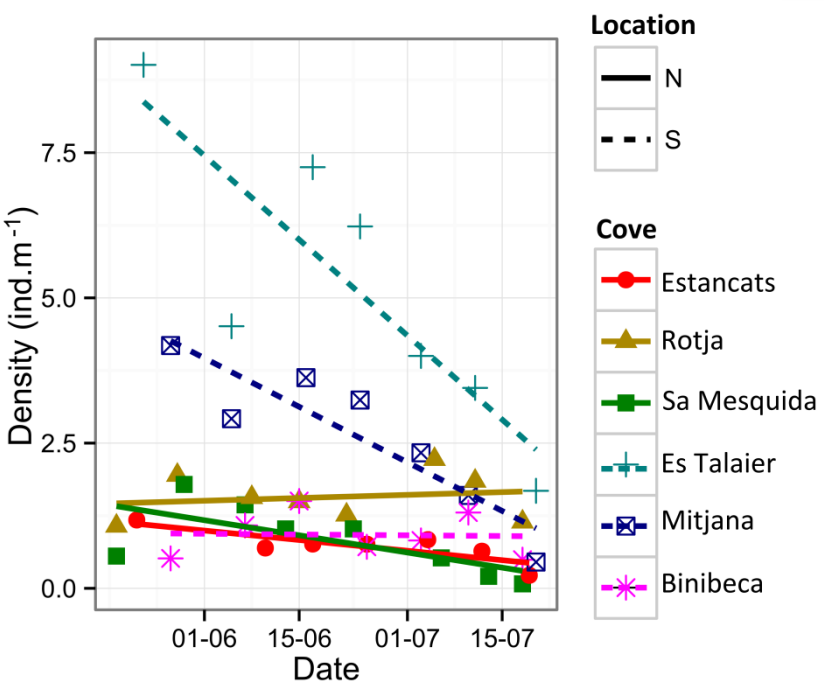

Fig. V-6. Observed data and predicted relationship of densities (ind.m^{-1}) of *Diplodus sargus* with time in each cove. Observed data=dots; predicted relationship =lines.

Table V-6. Results of the predicted relationship between densities of *Diplodus sargus* juveniles with time in each cove and results of the analysis of covariance (ANCOVA) comparing the densities (ind.m^{-1}) according to time and coves. a: intercept: b: slope; r^2: correlation coefficient; Df: degrees of freedom; MS: mean squared; F: statistic with its Degrees of freedom and its significance (· $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$).

Exposure	Location	Lineal Regression	a	b	r^2	F	P
Exposed	North	Estancats	1.156±0.151	-0.012±0.004	0.603	10.12 (1-5 DF)	**0.025***
		Rotja	1.460±0.293	0.003±0.008	-0.131	0.19 (1-6 DF)	0.678
		Sa Mesquida	1.432±0.316	-0.019±0.008	0.367	5.05 (1-6 DF)	**0.066·**
	South	Es Talaier	8.894±1.201	-0.103±0.029	0.652	12.26 (1-5 DF)	**0.017***
		Mitjana	4.799±0.518	-0.060±0.013	0.777	21.87 (1-5 DF)	**0.005****
		Binibeca	0.952±0.378	-0.001±0.009	-0.198	0.01 (1-5 DF)	0.928
ANCOVA			Df	MS	F	P	
Date			1	11.85	23.50	**<0.001*** **	
Cove			5	21.33	42.32	**<0.001*** **	
Date x cove			5	4.36	8.64	**<0.001*** **	
Residuals			32	0.50			

Table V-7. ANCOVA post-hoc Tukey HSD tests, comparing the juvenile densities of *Diplodus sargus* (ind.m^{-1}) according to time between pairs of coves. Significance (P): · $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Pairs of coves	P
Rotja-Estancats	0.400
Sa Mesquida-Estancats	1
Es Talaier-Estancats	**<0.001*** **
Mitjana-Estancats	**<0.001*** **
Binibeca-Estancats	0.997
Sa Mesquida-Rotja	0.330
Es Talaier-Rotja	**<0.001*** **
Mitjana-Rotja	0.036
Binibeca-Rotja	0.693
Es Talaier-Sa Mesquida	**<0.001*** **
Mitjana-Sa Mesquida	**<0.001*** **
Binibeca-Sa Mesquida	0.994
Mitjana-Es Talaier	**<0.001*** **
Binibeca-Es Talaier	**<0.001*** **
Binibeca-Mitjana	0.001

V.3.3. Juvenile ontogenetic changes in microhabitat use

Juveniles of most size-class differed in their density at the three microhabitats considered within each coves (PERMANOVA, Table V-8), except those in the size-class [55, 70). Furthermore, the interaction term between microhabitat and cove was not significant for each size class separately, thus indicated that tendencies of density distribution among microhabitats within the nursery coves were consistent across all coves (Fig. V-7).

Table V-8. PERMANOVAs table of results for *Diplodus sargus* juvenile densities in exposed coves in different microhabitats inside the nursery, for each size classes (mm TL): [10, 25), [25, 40), [40, 55), [55, 70). Significance: · P ≤ 0.1; * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

[10, 25) mm TL				
Source	df	MS	Pseudo-F	P(perm)
Microhabitat (mi)	2	63.42	5.64	**0.008****
Cove (co)	5	36.01	3.20	**0.016***
mi x co	9	12.53	1.11	0.335
Residuals	372	11.24		
Total	388			
[25, 40) mm TL				
Source	df	MS	Pseudo-F	P(perm)
Microhabitat (mi)	2	12.39	4.86	**0.008 ****
Cove (co)	5	18.32	7.19	**0.001*****
mi x co	9	2.94	1.16	0.327
Residuals	372	2.55		
Total	388			
[40, 55) mm TL				
Source	df	MS	Pseudo-F	P(perm)
Microhabitat (mi)	2	1.40	3.92	**0.024***
Cove (co)	5	0.81	2.25	**0.056·**
mi x co	9	0.47	1.30	0.218
Residuals	372	0.36		
Total	388			
[55, 70) mm TL				
Source	df	MS	Pseudo-F	P(perm)
Microhabitat (mi)	2	2.62·10-3	0.68	0.519
Cove (co)	5	1.09·10-2	2.80	**0.028***
mi x co	9	2.00·10-3	0.51	0. 828
Residuals	372	3.88·10-3		
Total	388			

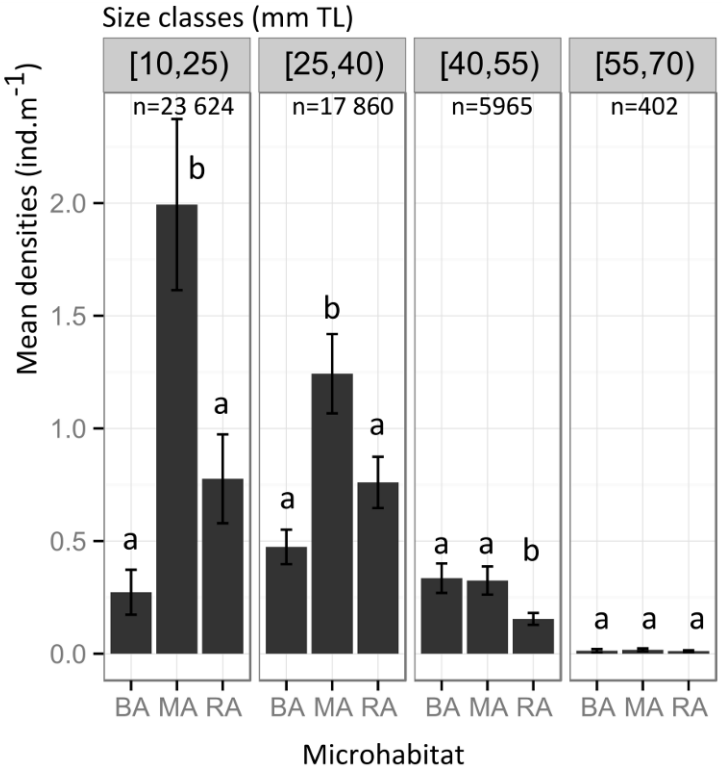

Fig. V-7. Patterns of *Diplodus sargus* juvenile densities among microhabitats (BA: Beach Area, MA: Mixed Area, RA: Rocky Area) of respectively size-classes: [10, 25), [25, 40), [40, 55) and [55, 70) mm TL; corresponding number of individuals (n) and pair-wise tests results between microhabitat levels are given (different lower case characters indicate significant density differences between micro-habitats).

Pair-wise comparisons of juvenile density between microhabitats types (Fig. V-7) revealed that juveniles within the [10, 25) and [25, 40) size classes were more abundant in mixed areas (MA) than in the beach areas (BA) or rocky areas (RA) (pair-wise habitat tests, $p < 0.05$). Fish of the [40-55) size-class were more abundant in both MA and BA than in RA ($p< 0.01$). Finally, fish of the [55, 70) size-class were homogeneously distributed in the three microhabitats (pair-wise test $p>0.1$).

V.4. DISCUSSION

According to our results, the settlement peak of *D. sargus* in Minorca is likely to be in May: indeed, peak density was clearly detected in 2012 in the mid-May, and in 2013 when we started our survey in the mid-May the density of 10-15 mm TL juveniles was already high. Conversely, it has been observed that settlement occurs mainly from June to July in the northern part of the western Mediterranean (Arceo et al., 2012; Bussotti and Guidetti, 2010; Di Franco et al., 2013; Macpherson, 1998; Macpherson et al., 1997; Vigliola et al., 1998) and in April in the south-west part of the basin (Félix-Hackradt et al., 2013a). This suggests a latitudinal variation in spawning and settlement, surely related to a latitudinal temperature gradient (Mouine et al., 2007).

Although the north and south shores may presumably be under the influence of different water masses of contrasted origins (Bethoux, 1980; López-Jurado et al., 2008; Millot, 1999; Pinardi and Masetti, 2000) we observed a synchronization of the settlement peak at both north and south coves both years (this chapter and see Chapter IV). One plausible explanation would be that settlers come from a common origin and reach nurseries synchronously because the mean distance between all the sampled coves was within the larval dispersal range reported for *D. sargus* (Di Franco et al., 2012). However in other areas, between sites separated by similar distances, such synchronization is less evident (Pastor, unpublished data). Currents coupled with the number and relative location of breeding areas as well as some environmental stimulus leading to a synchronous reproduction may play an important role in such synchronization patterns. Unfortunately, detailed knowledge of both coastal currents around Minorca island and natural *Diplodus sargus* breeding locations and biology are scarce (Vigliola, 1998).

Independently on the precise timing of the settlement peak at a regional level, the results reported here demonstrate that some of the seascape attributes considered in this study had a significant effect on settlement and post-settlement processes, particularly differences in cove exposure. At the island scale (several tens of kilometres), location of the coves in the north or the south coast had no major impact on the settlement peak nor on the recruitment level or on the growth rate of juvenile *D. sargus*. Nevertheless, coves in the south coast exhibited a higher variability in the density trends than those in the north, because of the

very high settlement peak in two south exposed coves ("Es Talaier" and "Mitjana"). It is worth to note that we observed a site-specific consistency in settlement intensity for one location ("Es Talaier") which displayed both in 2012 and 2013 the highest observed densities. Although this should be better investigated in Minorca island (i.e., more replicates are necessary), these kind of spatial consistencies of settlement peaks between years has been reported in other areas (Vigliola et al., 1998; Wennhage and Pihl, 2001). The site-specific variability (between coves) of the settlement peak has been attributed mainly to habitat structure although there are no studies which test it ((Cheminee et al., 2011; Vigliola et al., 1998). The two coves in the south shore with the highest settlement peaks displayed a highly heterogeneous habitat, with the patches of the three microhabitats lying in close quarters. Since habitat complexity and heterogeneity (*sensu* August (1983)) determine shelter and food availability and hence subsequent mortality and growth, it is plausible that the observed differences in settlement peak were due to such variability (Anderson and Millar, 2004; Félix-Hackradt et al., 2013b; García-Charton et al., 2004; Thiriet et al., 2014). Furthermore, this differences may be also related to the relative location and availability of nurseries *versus* spawning sites, coupled with differences in local hydrodynamics (Pineda et al., 2010; Roy, 2012). Indeed, the south, where the higher settlement peaks were recorded both in 2012 and 2013, the coast display a smaller amount of available nursery habitat than in the north part (see Chapter VI). In the south, this may lead juveniles to concentrate in the few available habitats, leading to the observed high densities.

At lower seascape scale (a few kilometers), settlement peak and density trends were controlled by exposure, as both the settlement and the recruitment peak were significantly higher at the exposed coves, independently on the location in the coastline. The density of juvenile *D. sargus* in the sheltered coves remained close to zero ind.m^{-1} throughout the whole sampling period. This suggested a positive influence of cove exposure on larval supply and subsequent settlement intensity. Although only a few studies have coupled hydrological regimes with bathymetry, topography and the distribution of fish eggs and larvae, available data indicate a match between the distribution of these spawning products and hydrodynamics (Brown et al., 2005; Jenkins et al. 1998; Martins et al., 2007; Pepin et al., 1995). It usually results into a low egg/larval supply to inner parts of the shoreline, e.g. the inner parts of the coral reefs systems (D'Alessandro et al., 2007), the upper reaches of

the estuaries (Bell et al., 1988; Martins et al. 2007) and the innermost part of bays. For this reason, settlement is favored in areas close to open waters, if suitable habitats exist (Brown et al., 2005; Jenkins et al., 1998; Pastor et al., 2013) This conceptual framework is consistent with the results reported here. Nevertheless, although a given degree of exposure may be favorable, it is worth notice that previous research on *D. sargus* also pointed out the preference of settlers for coast not only with gentle slope and heterogeneous boulders and pebbles bottoms, but as well protected from swell and strong hydrodynamics (i.e. coves) (Harmelin-Vivien et al., 1995). Vigliola's data (1998) even suggested that survival of *D. sargus* juveniles was favored in the most enclosed coves, through enhanced water temperature and consequent faster growth.

Once larvae have reached the nursery habitat and settlement is accomplished, post-settlement processes determine their survival and growth (Vigliola, 1998). In our study, recruitment level was compared using a crossed analysis (location x exposure), but very low numbers of juveniles occurred in sheltered coves, so the analyses of post-settlement dynamics were conducted only at the exposed coves. There, the growth of juveniles was similar between north and south coves and within the range reported by previous research for this species (Planes et al., 1999; Vigliola, 1998). This indicates that juvenile growth rate was independent on juvenile density, since large differences existed among coves in settlement peaks but juveniles grew at a similar rate everywhere. This is consistent with the density-independent growth reported in the previous chapter, but in contrast with the density-dependent growth patterns reported by Planes et al. (1998) for this species. This lack of density dependent for growth may suggest that food resources for juveniles were not a limiting factor, discarding a possible intraspecific competence for food resources (Hazlerigg et al., 2012; Shephard and Jackson, 2009).

Contrastingly, the rate of density decrease exhibited a strong density–dependent pattern, as juvenile density decreased faster in those coves where the settlement peak was the highest. As a result the recruitment level was similar at the six exposed coves. Density-dependent mortality has been described in previous studies about this species (Macpherson et al., 1997; Planes et al., 1998). Competence for food resources is not a likely cause, because of the density-independent growth rate reported above, and hence mortality by predation combined with competition for shelter stands as the main causes for the density dependent depletion of juveniles (Anderson, 2001; Forrester and Steele, 2000; Hixon and Jones,

2005). Exposure to wave action has been suggested to be a major factor in determining post-settlement losses in some cases (Jenkins et al., 1997). However, the exposed coves considered in this study displayed a much higher recruitment level than the sheltered ones. This is a direct consequence of the lower settlement peaks reported in sheltered coves, where density remained close to zero ind·m-1 through all sampling period, compared with exposed coves.

Previous research had reported a low density of adult *D. sargus* in suitable habitats in Minorca as compared with other adjoining regions (Cardona et al., 2013, 2007b; Coll et al., 2012), attributed to the oligotrophy of the coastal waters of the island and a limited larval supply (Cardona et al., 2007b). However, the results here reported, reveal that in some exposed coves of the south coast, the settlement peak is very high. Decoupling between larval supply, settlement and recruitment, have been frequently reported but no consensus has already been reached regarding the relative importance of settlement and post-settlement processes in determining recruitment (Di Franco et al., 2013; Félix-Hackradt et al., 2013a; Jenkins et al., 1998; Macpherson and Zika, 1999; Pineda et al., 2010). Available information (Planes et al. (1998); this study) indicates that, processes operating both at the settlement and post-settlement stage regulate the recruitment of *D. sargus*. However, topography may play a pivotal role by modulating the relative importance of both processes. Post-settlement processes such as density-dependent mortality may certainly result into major changes in juvenile density, but larval supply, determined in turn by cove exposure, stands as the main factor limiting the recruitment of *D. sargus*. Considering the scarcity of exposed coves along most of the south and northwest coast of Minorca (see as well Chapter VI), recruitment of *D. sargus* in the island might be limited not by oligotrophy, but because of the scarcity of nursery habitats in most of the coastline.

Finally, at the nursery scale (tens of meters), juveniles of different size classes were distributed differently across microhabitats. Smaller juveniles (i.e. settlers and juveniles <40 mm TL) were mainly localized in the mixed areas. As they grew up, they used as well the beach area in the same proportion and finally sub-adult fishes larger than >55 mm used equally all the microhabitats present inside the nurseries, without any preference. Since “mixed areas” usually occur in the more sheltered parts of the coves, Macpherson (1998) suggested for *D. sargus* a larval distribution mechanism related to slower water flow, similar to that reported by Breitburg et al. (1996). However, for other species, Dalgreen

and Eggleston (2000) suggested that ontogenetic changes of microhabitats aim to switch to the habitat displaying the better compromise between food availability and predation risk. Our observations might consequently be related to shelter availability, especially important in early juvenile stages (Sogard, 1997): more shelter may be provided by the more structured habitat (i.e. the mixed areas) at the beginning of *D. sargus* development in the nurseries. Furthermore, early individuals has been reported to feed mainly on harparticoids (Christensen, 1978) and some of our own unpublished data (see Appendix) reported in juveniles' stomach content and microhabitat food availability indicate a clear preference of smaller juveniles for harpacticoids usually found in the pebbles' and rocks' seaweeds, rather than interstitial harpacticoids which inhabit the sand. Furthermore, this stomach contents data revealed a presence of insects and mites which were probably eaten in the water column or at the water surface. Posteriorly, older juvenile fish, less vulnerable (>40 mm) may explore new habitat with less shelter (Anderson, 1988; Sogard, 1997). They may begin to move to other microhabitats inside the cove (such as beach or rocky areas), displaying a homerange expansion, habitat diversification, diet diversification, and starting their emigration out of the nursery (Christensen, 1978; Macpherson, 1998; Vigliola and Harmelin-Vivien, 2001).

V.5. CONCLUSIONS

To sum up, the results reported here indicate that factors and processes operating both at settlement and after settlement determine the density and growth of juvenile *D. sargus*. Exposure determines the magnitude of the settlement peak and, secondarily, a very low recruitment peak in those coves with a very small supply of settlers. Density-dependent mortality determines the recruitment peak in exposed coves with a high supply of settlers, thus resulting in partial decoupling between settlement and recruitment. From the management perspective, we may conclude that exposed coves are the main nursery habitats for *D. sargus* and that total recruitment might be limited by the scarcity of suitable habitats, mainly along the south coast of the island.

Chapter VI. General Discussion

Photo VI-1. *Sargantana I*. Boat of Estació d´Investigació Jaume Ferrer at Fornells Bay, Minorca island. October 2012. Photo: Amalia Cuadros.

Chapter VI. General Discussion

VI.1. DISCUSSION

VI.1.1. Patterns

This thesis has focused on the juvenile fish assemblage of three of the major shallow habitats occurring in the Mediterranean Sea: seagrass meadows, rocky bottoms with canopy forming macroalgae and mixed bottoms of sand, pebbles and rocks. These three habitats support more abundant and diversified juvenile fish assemblages as compared with others shallow infralittoral benthic habitats such as sandy bottoms (Guidetti, 2000), Chlorobionts meadows (Cheminée et al., in press), barren grounds (Thiriet, 2014), or shrubland (Cheminée et al., 2013; Thiriet, 2014). Furthermore, the present thesis used *Diplodus sargus* as a model species to understand the relative importance of the settlement and post-settlement processes at the species level.

The results showed that habitat type is a major determinant of the composition of the juvenile fish assemblage, because the three considered habitats shared many species, but differed dramatically in the density of some dominant species. Nevertheless, the three considered habitats exhibited also a large amount of variability in their three-dimensional structure, which in turn was a second major source of variability for the density of juvenile fishes.

Mediterranean seagrass meadows, including those formed by *Cymodocea nodosa*, have long been recognized as important nursery habitats for *D. annularis*, *Spondyliosoma cantharus* and *Symphodus cinereus*, whereas other species prefer other infralittoral habitats (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995). Actually the juveniles of other species occur in seagrass meadows at a much lower density than in rocky habitats covered by canopy forming macroalgae and indeed the presence of boulders scattered within the meadows is the major source of spatial variability within seagrass meadows, as it largely increased the abundance of some species typically associated to rocky bottoms. We argue that this small boulders improve the habitat quality of the

seagrass meadow, increasing the available resources and at the same time generating small ecotones, i.e., edges within the seagrass meadow where organisms may regularly switch between habitats and therefore exploit alternatively the optimum micro-habitat as regards to food or shelter (Cheminée et al., in press). Furthermore, although our sampling design did not enable us to test it, distance to open water systems is another major potential source of variability for the juveniles fish assemble inhabiting meadows in sheltered bays, because of differences in the input of larvae and eggs (Brown et al., 2005; Francour, 1997; Jenkins et al., 1998; Martins et al., 2007; Montgomery et al., 2001; Pastor et al., 2013).

Rocky habitats with arborescent, erect and perennial canopy forming macroalgae are widely recognized to be important nursery habitats for many species worldwide (Jones, 1984). In the Mediterranean Sea, the highest density of juvenile labrids is reported from *Cystoseira* forests (Bussotti and Guidetti, 2010; Cheminée, 2012; García-Rubies and Macpherson, 1995). However, the distribution of juveniles within *Cystoseira* forests had been poorly studied previously and the results reported in this thesis demonstrates that their juvenile fish assemblages changed according to both depth and canopy structure, with species differing in their depth and canopy structure preferences.

Finally, shallow mixed bottoms of sand, pebbles and rocks within coves are known to be major nursery habitats for *D. sargus*, *D. puntazzo*, *D. vulgaris* and *D. cervinus*, since those species settle and are more abundant in those habitat than anywhere else (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). However, a large variability in the density of *Diplodus* spp. juveniles has been reported from sites sharing this kind of habitat (Arceo et al., 2012; Di Franco et al., 2013; Vigliola et al., 1998). Previous studies suggest that seascape features at different spatial scales may explain such spatial variability, notably, hydrodynamism, depth and habitat heterogeneity (Cheminee et al., 2011; Di Franco et al., 2013; Vigliola, 1998; Vigliola et al., 1998). In this thesis we demonstrated that three factors operated to determine the abundance of juvenile white sea breams in coves in Minorca island: regional coast configuration (north vs. south oriented), cove local configuration (exposed vs. sheltered) and availability of heterogeneous substratum. Furthermore, post-settlement processes within coves strongly influenced the spatial density patterns, as previously reported elsewhere (Macpherson et al., 1997; Planes et al., 1998).

Hence, this thesis shows that the spatial variability in the density of juveniles fishes in the shallow infralittoral habitats of Minorca island results not only from differences in habitat type but also from processes operating at various spatial scales within any habitat. Firstly, the general coastal configuration is the main determinant of the juvenile density occurring in regions more than 5 km apart, as shown by the differences in the density of *D. sargus* in coves in the north and south coast of the island. Secondly, the variation of the juvenile density between sites only 1-3 km apart is influenced both by local coast configuration and by differences on habitat structure. For example, in Fornells Bay, juvenile density variations between sites may be mainly due to the relative location of each site within the bay and the distance to the open sea (Chapter II). *D. sargus* density variations between closely located sites is explained by coast configuration (with or without line of sight to open sea) and also by the relative abundance of heterogeneous substrate within each cove. Finally, at a scale of less than 500 meters, habitat structure determined the spatial variability of juvenile densities and the composition of juvenile assemblages. This was illustrated in Chapter II Chapter III and IV by the influence of boulders on the juveniles fish community from seagrass meadows, by the responses of the juvenile fish assemblage to variations of the *Cystoseira* canopy structure and by the relationship between juvenile distribution within coves and the relative abundance of sand or rocks inside the coves. Finally, no patters in juvenile density were observed at scales lees than 1 m, which suggests that no process operates at that scale.

VI.1.2. Underlying processes

When observing these density patterns, we may try to understand what the underlying processes are. Larval dispersal is the main process which acts at the largest spatial scale in determining juvenile density distributions since it shapes initial settlers input (Cowen and Sponaugle, 2009; Peck et al., 2012; Pineda et al., 2010). Various processes influence larval dispersal, mainly larval features (behavior, swimming capabilities and physiology) and hydrodynamism (Fisher, 2005; Gerlach et al., 2006; Pineda et al., 2010; Simpson et al., 2005; Ware, 1975). The relative importance of larval features and hydrodynamism are often disputed (Cowen and Sponaugle, 2009), since some authors supports that larvae could be considered mainly passive particles in the ocean (James et al., 2002; Lobel and Robinson, 1983), whereas others state that larvae could not be considered as mere particles

and are able to influence their transport (Berumen et al., 2012; Bradbury et al., 2008; Gerlach et al., 2006; Montgomery et al., 2006; Mouritsen et al., 2013; Norcross and Shaw, 1984).

Here, in Chapter IV, we highlighted the vulnerability of postlarvae to hydrodynamic conditions. Such hydrodynamic conditions are shaped by larger seascape features. The configuration of the coastline determines the influence of winds and the associated surface currents. Weak winds from sea to coast generate adequate currents which favored the larval supply at coast, according to previous works (Raventos and Macpherson, 2005; Vigliola, 1998). Furthermore, in semi-enclosed coves and bays with a low water turnover, surface currents may not able to guarantee larval supply processes (Chapter V). However, larvae should not necessarily be considered passive drifters; indeed, when currents may favor the settlement in a given bay, juveniles may select, or alternatively suffer lower mortalities, in areas near the mouth of the embayment as reported in previous works (Brown et al., 2005; Francour, 1997; Jenkins et al., 1998; Martins et al., 2007; Montgomery et al., 2001; Pastor et al., 2013) (see also Chapter V and discussion of Chapter II).

Once larvae reach a given benthic area, density of juveniles changes according to habitat types and depth, as juveniles seem to be strongly associated to limited habitat types within narrow depth ranges (Biagi et al., 2011; Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995). Furthermore, within a given habitat type juveniles may select patches of a given tri-dimensional structure among the selected habitat, e.g. a given level of macrophyte density (Bell and Westoby, 1986a; Cheminée et al., 2013). Such patterns (differential distribution of juveniles according to depth, habitat type or among a given habitat between patches of different structuration levels) may be explained by two alternative processes: active habitat selection or differential mortality rates. In fact, Thiriet (2014) showed that both types of processes act simultaneously in determining juvenile density patterns.

Juveniles in early stages are the most vulnerable to predation (Sogard, 1997) since at such stages juvenile's movement capacity is low, as compared with older stages of the fish life cycle, and their small size make them being suitable prey for a broad range of predators (Scharf et al., 2000). In this sense, being closely associated to a given habitat structure or to shallow depths may facilitate the sheltering of juveniles (Behrents, 1987; Hixon and Beets,

1989; Paterson and Whitfield, 2000; Shulman, 1985). Furthermore, highly structured habitats, such as seagrass meadows, seaweed forest and mixed bottoms are argued to proportionate high food availability (Ballesteros, 1990a, 1990b, 1988; Borowitzka et al., 1990; Mazzella et al., 1998; Pitacco et al., 2014; Sánchez-Jerez et al., 1999)(see also Nina-Larissa Arroyo *et al* in prep.). Such habitats may enhance foraging efficiency, which provide a fast juvenile growth that will make juveniles less vulnerable to predation or competition (Connolly, 1994; Tupper and Boutilier, 1995, 1997). Fish density patterns may consequently respond to the trade-off hypothesis, which states that the optimal habitat at a given life stage optimizes low predation risk and higher food availability (Dahlgren and Eggleston, 2000). However, we observed that not all species and not all juvenile stages preferred structured *vs* less structured habitats or patches among a given habitat. In fact, some species are morphologically adapted to forage or avoid predators in a more structured patches inside the habitat, whereas others are adapted to less structured, or even bare habitats (Hoar and Randall, 1979; Keast and Deirdre, 2011; Leis et al., 2011; Motta et al., 1995; Recasens et al., 2006). In this sense, the morphology of the fish body is a key feature to understand such patterns. Deep bodies are adapted to forage and shelter within more structured habitats (e.g. *Symphodus* spp.), whereas streamlined bodies are adapted to forage in less structured habitats such as the the edge or the top of the macrophyte canopy (e.g *Coris julis*, *Thalassoma pavo*, *D. annularis*). Furthermore, colour patterns and also mobility strategies help fish differentially to better hide or forage in different habitats structure (Houtman and Dill, 1994; Main, 1987; Marshall, 2000; Tallmark and Evans, 1986). For example juveniles of *Symphodus* spp. are pale brown, which fits with the brown colour of the Fucales canopy or substratum, although sometimes they are more green (personal observation) fitting with seagrass canopies. Many Gobiidae, Blenniidae and Tripterygiidae are present in denudated substrata, and their colour fits with the sand, moody or rocky substratum (Patzner, 1999). Its tactic to avoid predators is to remains quiet (Tallmark and Evans, 1986). Other species, even mobile ones, are golden coloured at early stages, e.g. *Salpa sarpa*, *D. annularis*, *S. cantharus*: such colour patterns may help to camouflage in the silvery-yellowish environment of shallow seagrass meadows, where golden reflex formed by the sun, and / or mixed with the seagrass colours difficult their detection. Other mobile species, such as *D. sargus* or *D. vulgaris*, are almost transparent or pale gray at early stages, and are difficult to detect in sandy environments where they use to settle. In any case, dependency on highly structured environments relaxes as juvenile

grow (Macpherson, 1998), probably because they become more mobile, and consequently they theoretically can escape more easily from predators. Nevertheless, more studies are needed to couple juvenile fish morphology and habitat use.

Obviously, larval dispersal and supply operate at a much larger scale than habitat selection or differential mortality, which explains why juvenile fish densities also vary at different spatial scales depending on coast configuration and habitat structure. However the influence of such factors may depend on the seascape perception of fish, which changes according to species (Morris, 1987; Turner et al., 1995). For instance, *S. ocellatus* has a planktonic larval duration (PLD) of 9 days, whereas that of *Lipophrys trigloides* is up to 71 days (Raventos and Macpherson, 2001); for the latter species, which dispersal is longer, seascape features at larger scales may be more important than for *S. ocellatus*. However, juveniles of *Lipophrys* present a reduced mobility (Faria et al., 1998), they seems to be less mobile than *S. ocellatus* (pers. observation), i.e. exploring daily a smaller areas, consequently they may perceive habitat structure at finer scales than *S. ocellatus*. Furthermore, this seascape perception changes as a function of the size of juveniles, as illustrated for example by the case of *D. sargus* juveniles (Macpherson, 1998) (see also Chapter V).

Additionally to the influence of seascape at different scales on settlement processes, post-settlement processes such as density-dependent mortality, strongly influences the final production of juveniles (Juanes, 2007; Macpherson et al., 1997). Density-dependent mortality processes has been explained by both competency and predation processes, which causes juvenile mortality (Hixon and Jones, 2005). It has been argued that this density-dependency is typical of site attached residents species (Planes et al., 2000). In the case of sea breams (Sparidae), previous work highlighted that density-dependent mortality is a major process shaping its juvenile populations (Félix-Hackradt et al., 2013a; Macpherson et al., 1997; Planes et al., 1998). Our results support this conclusion (see Chapters IV and V), but in Chapter V we highlighted that even if denso-dependent processes may strongly influence the final production of juveniles, the seascape configuration could be the major limiting factor in the final production of juveniles. Density-dependent mortality has been less studied in labrids but some species seems to present a density-dependent mortality whereas others may display a density independent mortality (Félix-Hackradt et al., 2013a).

Predation and competition are key factors influencing juvenile density (Jones, 1987; Sogard and Olla, 1993) and in chapter III we aimed to test if interactions with adults and predators had any effect on juvenile distribution. However the densities of predators were very low in the studied area and juveniles and conspecific adults didn't display any spatial partitioning, thus suggesting that these factors were not relevant in this case (Chapter III).

VI.1.3. Coastal management

Juvenile densities are determined by the interaction of a large number of factors: spawning success, food availability, physical-chemical conditions, predation, competency, the relative location between adult and juvenile habitats, the influence of neighbouring habitats, fish behaviours and morphology, etc. (Beck et al., 2001; Horinouchi, 2007). From the coastal management point of view, in front of the vast number of factors which could influence nursery value of a given habitat, it is difficult to take all of them into account, especially considering the scarce knowledge that we have about the influence of most of them. From a management point of view, a reasonable starting point may be to take into account and guarantee at least the availability of essential habitats.

Nevertheless, juvenile habitats are usually not considered in management practices, as illustrated by some examples. For instance, in Minorca island, according to the definition of *Diplodu*s nursery habitat (Harmelin-Vivien et al., 1995), only ~9 % of all the coastline may be considered as potential nurseries for *D. sargu*s, *D. vulgaris*, *D. cervinus* and *D. puntazzo* (Fig. VI-1 and Fig. VI-2; Cuadros et al., unpublished data), all of them of commercial and recreational interest and with an important ecological role (Giakoumi et al., 2012; Guidetti, 2006; Lloret et al., 2008). Furthermore, ~15% of these potential nurseries are coves without line of sight to open sea, expected to produce very low numbers of juveniles (Chapter V) and less than a quarter of these potential nurseries are located inside a protected area (Cuadros et al., unpublished data). In other regions where potential nurseries have been estimated, it is also reported a very low number of potential nurseries as respect to the entire shoreline. For example, in the Marseilles area (France), only ~10 % of the shoreline is considered as suitable nursery habitat for these species, and less than half of they are located in protected areas (Cheminée et al., 2014). Similarly, along the 300 km of Catalan coastline (from Roses to Leucate), only ~25% of the coast

displays nursery habitats for *Diplodus* spp. and only a quarter of it is located in protected areas (Zawadzki, 2015).

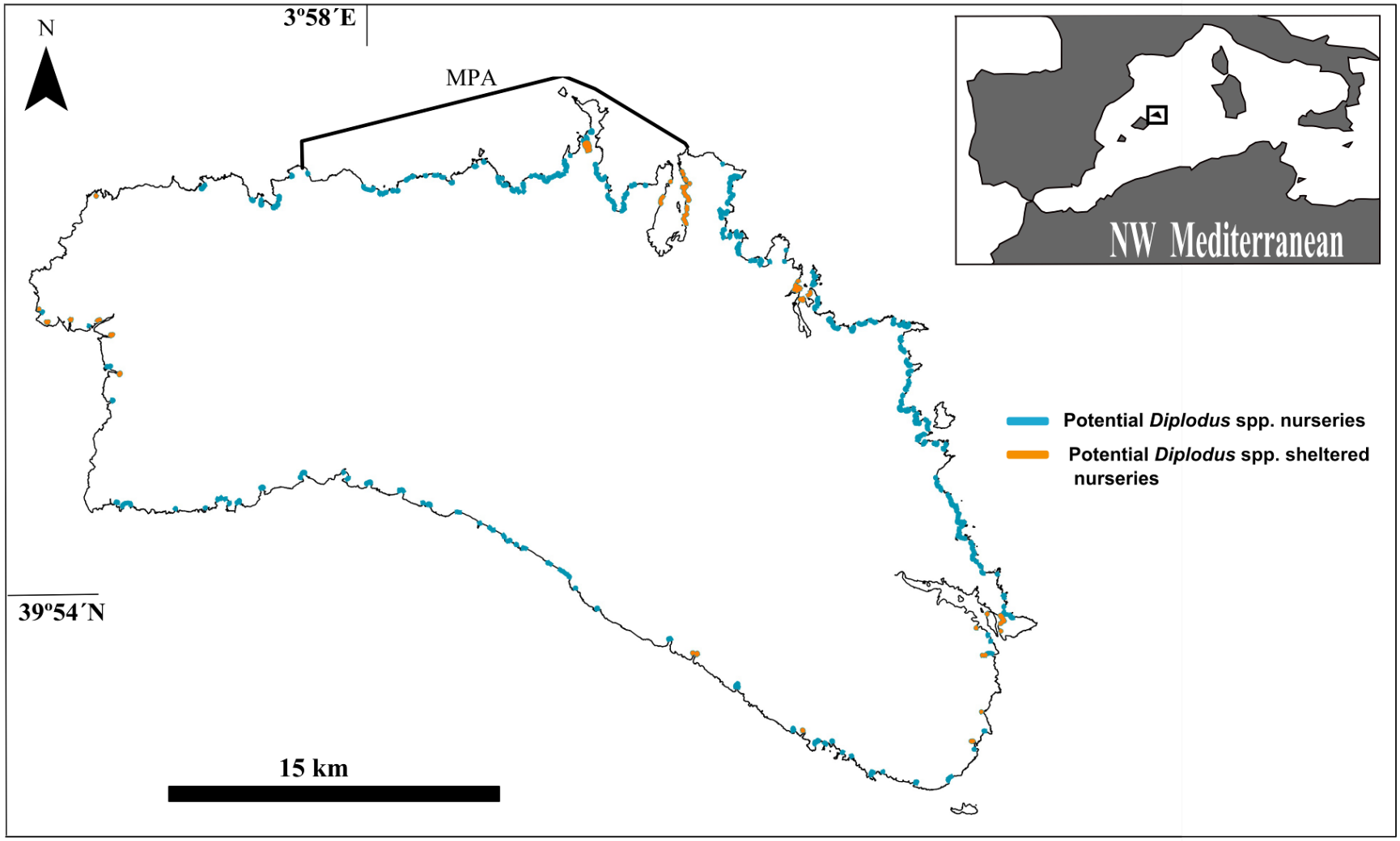

Fig. VI-1. Potential nurseries of *Diplodus sargus*, *D. puntazzo*, *D. vulgaris* and *D. cervinus* in Minorca island (coloured segments). Nursery habitats for these species: mixed bottoms of sand, pebbles and boulders (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). Sheltered nurseries are highlighted (in orange). MPA: Marine Protected Area.

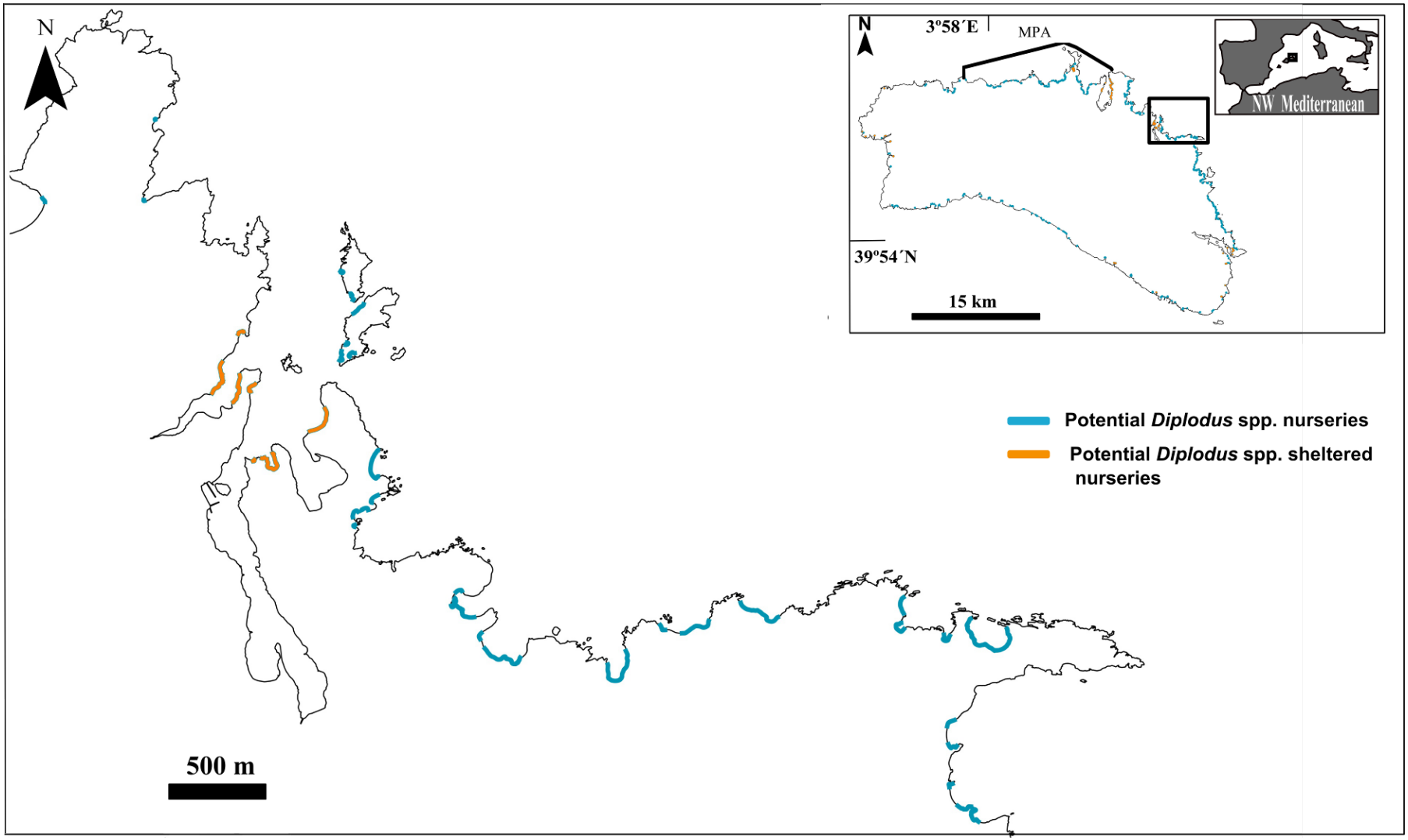

Fig. VI-2. Detail of the potential nurseries of *Diplodus sargus*, *D. puntazzo*, *D. vulgaris* and *D. cervinus* in Minorca island (coloured segments). A part (black rectangle) of Minorca island shoreline. Sheltered nurseries are highlighted (in orange). MPA: Marine Protected Area.

Consequently, in Minorca island and elsewhere, *Diplodus* nurseries (the shallow heterogeneous bottoms) represent a small proportion of the coast, and the most part of them are located outside marine protected areas. Besides, even if located within MPAs, in most of the MPAs, regulation managements in protected areas are centred in fishery banning. For the protection of juveniles, since they are not-targeted sizes for fishery (García-Charton et al., 2008), the physical protection of habitats should be the most important management action (Cheminée, 2012). Indeed, in the Mediterranean, these nurseries tend to be physically destroyed even in protected areas, due to coastal development project and physical construction on them (Cheminée et al., 2014; Meinesz et al., 2006). Furthermore, beach management planning through all Mediterranean coasts usually never take into account the nursery habitats of this species. Indeed, classical beach management is restricted to the protection of dune systems, and possible associated wet-lands, the limitation of anchoring in seagrass meadows, and the removing by heavy machinery (tracks, tractors, etc.) of the cast material of seagrass deposited along the shoreline (Borum et al., 2004; Silva et al., 2007; Van der Meulen and Salman, 1996). Beach nourishment projects are an usual practice in Europe and worldwide (Davison et al., 1992; Hanson et al., 2002) and may potentially affect broadly the replenishment of *Diplodus* spp. species, since homogenises the sea bed in coves, and consequently causes the disappearance of the juvenile habitat, i.e., the heterogeneous mixed bottoms with pebbles, boulders and rocks.

As a regards to *C. nodosa* seagrass, in Minorca island, Fornells Bay is one of the areas with the most extensive *C. nodosa* meadows (U.T.E. Intecsa-Inarsa, s.a, 2008), intermingled with *Posidonia oceanica* meadows in the deepest parts of the bay. A reserve area was created in this bay due to the good conservation status of their meadows, but also due to their potential ecological value as nursery habitat for fishes (Manent and Abella, 2005). However, the most protected area is the innermost part of the bay, although the highest abundance and richness of juveniles were found near the entrance of the bay, as suggested by previous works (CAIB, 2015) and confirmed in the present thesis. Besides of this, in this case again, management in the bay is restricted to fishery banning, and thus juveniles are not a priory affected by this regulation measures since they are not targeted by fishermen (García-Charton et al., 2008). Furthermore, although anchoring in *P. oceanica* meadows is forbidden in the entire bay, it is still allowed in *C. nodosa* meadows, which

occupy at least one half of the bay (U.T.E. Intecsa-Inarsa, s.a, 2008). Besides, harbour development in the bay is a potential threat.

Finally, as a regards to *Cystoseira* forests, in spite of their importance as nursery habitats for many labrids (Chapter III and previous studies e.g. Thiriet, 2014), it is still not being prioritized in the European Habitats Directive.

These examples highlight that protection or management plans usually do not take into account juvenile habitats, or even if theoretically some plans are established to protect juvenile areas, such as in Fornells bay, management zoning and actions are designed without establishing measures which effectively affect juveniles. We still do not know to what extent the unprotection of juvenile habitats is influencing the replenishment of adult populations, but if management practices do not specifically protect juvenile habitats we face the risk to compromise the replenishment of adult populations, including economically and ecologically relevant ones.

Furthermore, if future management practices are designed with the aim to protect juvenile habitats, it is important to take into account some issues for avoiding the preferential selection of some habitats *versus* others, without being fully aware of the underlying processes. For example, in Fornells bay, *P. oceanica* meadows are protected from anchoring, but *C. nodosa* meadows are not. However, studies which compare the nursery role of both habitats are scarce. We still don't know the relative importance of each habitat for juveniles. A necessary first step in management actions will be the improving of our knowledge about juvenile habitats in Mediterranean Sea in order to avoid the exclusion of some potential and valuable nursery habitats in management plans.

Moreover, since the Mediterranean seagrass meadows are preferential nursery habitats for a only a very few species, they have been considered less relevant than *Cystoseira* forests (Bussotti and Guidetti, 2010; Franco et al., 2006; García-Rubies and Macpherson, 1995), but see Guidetti (2000). This is sharp contrast with the relevance of seagrass as nurseries in other regions worldwide (Heck et al., 2003). We did not compare directly the abundance of juvenile fishes in *Cymodocea* meadows and *Cystoseira* forests, but we recorded much higher total abundances of juveniles in *Cystoseira* forests than in *Cymodocea* meadows (4.42 to 11.37 fish.m^{-2} in *Cystoseira* forests *versus* 0.35 fish.m^{-2} in *Cymodocea* meadows, all in September). Similarly, Guidetti and Bussoti (2000), in mixed meadows of *C. nodosa* and *Z. noltii,* recorded 0.22 juvenile fish.m^{-2}. Le Direach et al (2015) recorded ~0.6 fish.m^{-}

^{2} in both *Cymodocea* and *Posidonia*, and ~2.2 fish.m^{-2} in *Cystoseira* forests. Cheminée (2012), in a study with artificial habitat mimicking dense *Cystoseira* forests, recorded 7-10 juvenile fish.m^{-2}. Thus, the overall evidence shows that *Cystoseira* forests harbour a higher total juvenile density than seagrass meadows. Besides, mixed heterogeneous bottoms seem to be as well important only for a low number of species, mainly *Diplodus* spp.), thus highlighting the relevance of *Cystoseira* forests. However, these must be taken with caution because of three reasons.

Firstly, although several species seem to be more abundant in *Cystoseira* forest, when we compare this habitat with seagrass meadows, only in terms of presence of species, many species may be present in both habitats. Even more, seagrass meadows may display more number of taxa as observed in other works (Le Diréach et al., 2015).

Secondly, seagrass and mixed bottoms seems to be essential at least for sparids, whereas *Cystoseira* forests seems to be essential for labrids (Bussotti and Guidetti, 2010; García-Rubies and Macpherson, 1995). In this thesis 77-58 % of recorded taxa in *Cystoseira* forests belonged to labrids, whereas only 15-24 % belonged to sparids. Contrarily, in *Cymodocea* meadows 58.03% of the recorded taxa belonged to sparids whereas 37.15% of recorded taxa belonged to labrids. Usually, some species occurs primarily in one of two habitats (e.g. in this thesis juvenile *D. annularis* and *L. mormyrus* were only present in seagrass meadows and juvenile *T. pavo* were only present in *Cystoseira* forests). In this sense the un-protection of one of these habitats (instead of protecting all) would lead to the unprotection of the associated species, which even if may be only a few, are important from ecological and economical point of view. Since there is not one single habitat that includes all species, and since different species require different habitats, the protection of fish biodiversity requires, from a management point of view, to protect a diverse mosaic of habitats in the seascape of a given region.

Thirdly, habitat availability in each region must be taken into account. Indeed, even if one habitat may display higher juvenile densities of some species, this habitat could be scarce in a given region and thus produce overall less juveniles than other habitats. For instance, in Minorca rocky reefs with photophilic algae, including *Cystoseira* forests, occupy only ~16% of the infralittoral shallower than 25 m, whereas seagrass meadows occupy ~84% (~3% *C. nodosa* and 81% *P. oceanica*) of the same part of the infralittoral of the island (Fig. VI-3 and Fig. VI-4). If only areas shallower than 15 m are considered, rocky reefs

with photophilic algae are dominant over seagrass meadows (~60% vs ~40 %, respectively), although truly extensive *Cystoseira* forests occur mainly along the northern coast, in some areas (Sales, pers. comm.).

In this sense, although seagrass may be less productive per unit area, they may have a net production of juveniles equivalent to that of the *Cystoseira* forests around the island. Thus, even habitats that may have a small per-unit-area contribution to fish recruitment may be critical for sustaining adult populations (Dahlgren et al., 2006). Consequently, when juveniles may be present in various habitats, the availability of each habitat in each region must be taken into account to elucidate the real importance of each habitat, in each area, in producing juveniles. In an extreme scenario, the protection of only the habitat which theoretically produces more juveniles, may lead to the unprotection of other more extensively present habitats, which disappearance may deplete significantly the production of juveniles. In this sense, the extrapolation of what happens in one site to another site does not necessarily works.

Finally, from a management point of view it is important to consider that the fulfillment of the contrasted needs of the different species is reached by the availability of different habitats, but also by the natural structural variability among each habitat, which generates more or less structured patches (Chapters II and III). This natural variability favored species richness. Natural processes generate variations of habitat heterogeneity or complexity at very large scale or contrarily at lower scales. For example, in *Cystoseira* forests, geomorphology is constant over hundreds of years and generate variations of substrate complexity or heterogeneity at large scales along the northern coast of Minorca island, whereas overgrazing, generating barren grounds, adds an overlapping level of variability at a smaller and shorter spatial and temporal scales respectively (Cardona et al., 2013, 2007b). Organisms take advantage of this natural variability as a function of both their seascape or habitat heterogeneity-complexity perception which change according to species and life cycle-stages (Cooper et al., 1998; Morris, 1987; Turner et al., 1995). For maintaining species biodiversity is not correct considering densest forest are the best ecosystem and that barren grounds are the worst ones (Cardona et al., 2007b).

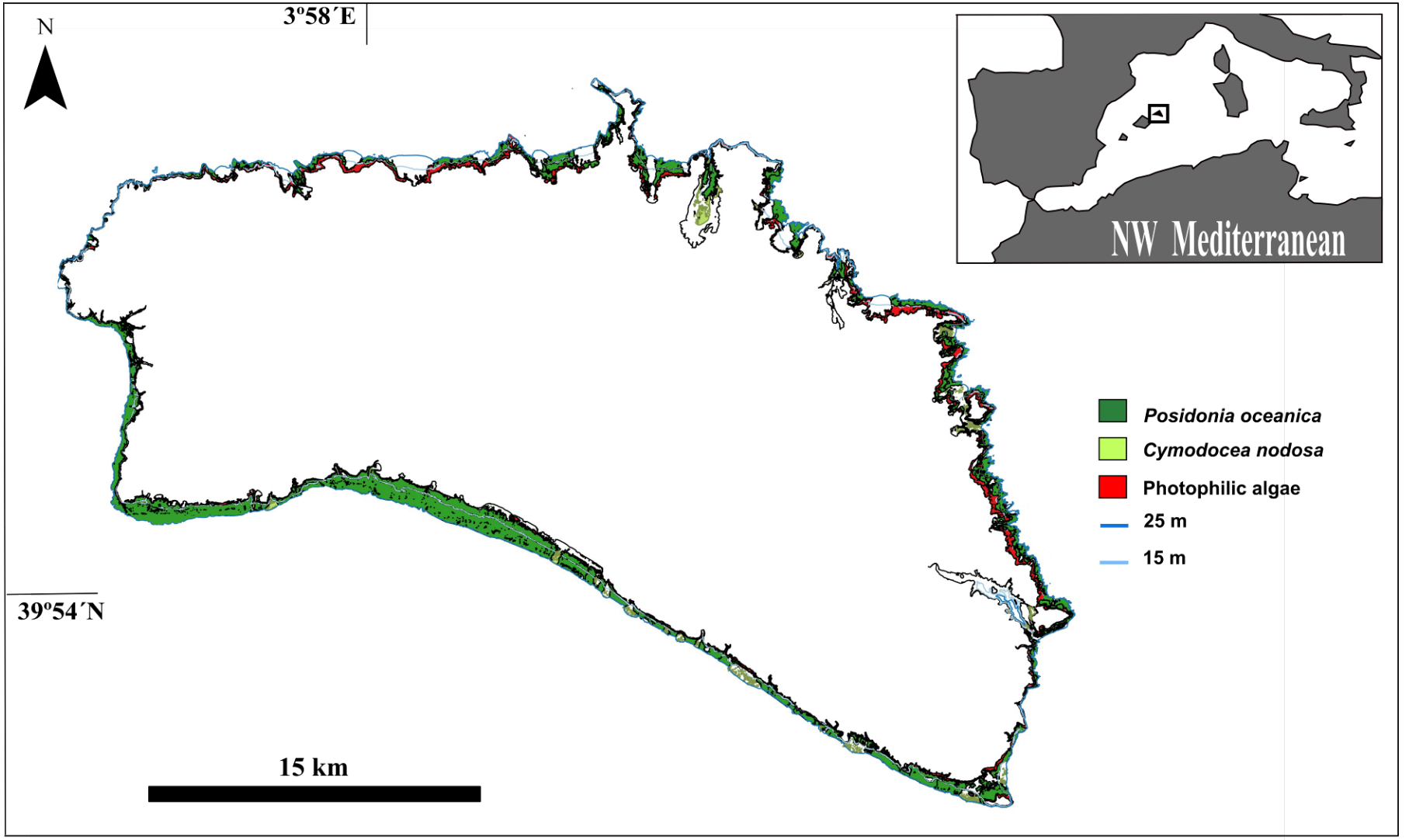

Fig. VI-3. Biocenosis of Minorca island in the infralittoral from 0 to 25 m depth.

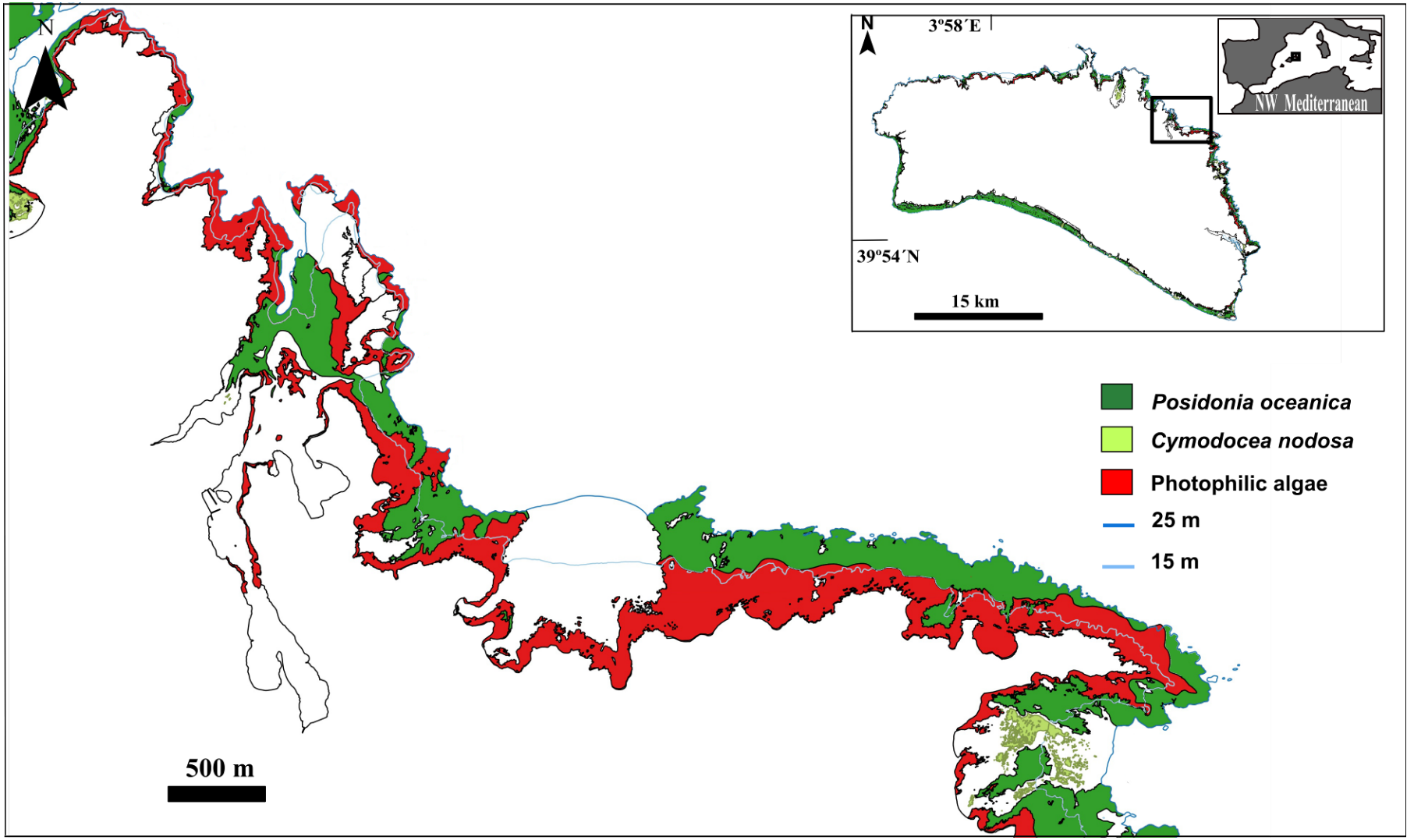

Fig. VI-4. Detail of the biocenosis of Minorca island, in the infralittoral from 0 to 25 m depth. A part (black rectangle) of the island shoreline to better appreciate each biocenosis.

Human stressors often homogenize and simplify seascapes, which may result in a scarcity of certain nursery habitats. For example, the presence of ports homogenised bottoms worldwide, generating muddy seascapes at ports and adjacent areas (Boudouresque et al., 2006; Reise, 2005); in the same way, the invasive algae, *Caulerpa taxifolia*, has homogenised 131 km^2 of benthos in the NW Mediterranean sea until 2000 (Meinesz et al., 2001); pollution and associated habitat destruction caused the disappearance of wide *Cystoseira* forests along French and Spanish continental shores (Thibaut et al., 2014), thus simplifying them. In fact, many strong disturbances of natural ecosystems have a human origin (Foley et al., 2005; Jackson et al., 2001; Vitousek et al., 1997), and cause loss of biodiversity, whereas less intense disturbances, moderated, favoured biodiversity because it promotes greater landscape heterogeneity (Roberts and Gilliam, 1995; Roxburgh et al., 2004; Townsend et al., 1997). These kinds of moderate disturbances, less intense, are usually of a natural origin (Connell, 1978).

However, the rational use of sea resources by humans may as well generate less intense disturbances, having beneficial effects for the economy and the ecosystem, as it has been proved in continental landscape areas. In terrestrial ecosystems, e.g. although intensive agriculture and livestock cause significant losses in habitats, traditional, extensive agriculture and livestock husbandry can be beneficial (Olea and Mateo-Tomás, 2009) since they support a wide range of species, including those unique from natural habitats (MacDonald et al., 2000). Therefore it is essential to define the uses that are considered moderate to conduct proper management of natural areas, in order to protect biodiversity and ecosystems, and to continue being able to use natural resources through the future.

VI.2. PRELIMINARY CONCLUSIONS

Juveniles replenish adult populations, and therefore they are essential for the preservation of biodiversity, and to ensure the conservation of species with both ecological and economic interest. Consequently, the interest in juveniles and their habitats has increased worldwide in action plans of coastal managers and among the scientific community. However, very few is known about the ecology of Mediterranean juvenile fishes yet. Essential habitats for juveniles are not fully investigated and the factors which influence the final production of juveniles are not well understood yet. The results of this thesis have contributed to the improvement of the knowledge of the ecology of juvenile fish, through the improved understanding of factors that influence the production of juveniles in three common Mediterranean habitats: *Cymodocea nodosa* meadows, *Cystoseira* forests and mixed bottoms of sand, pebbles, and boulders.

Collected data either of juveniles' densities or behaviors, in Chapters II to V -and results reported from the bibliography-, show the importance of the three-dimensional environment structure *sensu lato* at different spatial scales, from the three-dimensional configuration of the coast to the configuration of a given habitat. Consequently, from the juveniles point of view, in order to manage a given locality, a multi-scale approach is necessary.

At larger scales, first, the coast configuration may be considered, since it may determine a lower number of juveniles. Secondly, at the seascape scale, areas with a heterogeneous mosaic of habitats must be selected; doing so will guarantee the fulfilling of the contrasted needs of different species, with different nursery habitats.

Thirdly, in the given locality considered, it must be taken into account the relative availability of the habitats in the seascape. Indeed, in theory, the optimal production of juvenile must be achieved through including the adequate surface of each habitat in the seascape, taking into account the theoretical taxa-specific nursery value of each one, i.e. their relative per unit area productivity in the locality.

At lower scales, among the mosaic of a given locality, each habitat should be protected including its intrinsic natural variability in its three-dimensional structure. Monotonous bottoms, e.g. artificially homogenized ones, should be avoided, since the optimum

production of juveniles of different species in a given habitat seems acquired through the intrinsic patchy nature of a given habitat, displaying a mosaic of various habitat characteristics (e.g. canopy cover), and therefore fulfilling the contrasted needs of different species which inhabit a given habitat.

MPAs may be a tool to physically protect the essential habitats, if adequate regulation is applied. Besides, as a general rule for coastal management and in order to guarantee an optimal juvenile production, in or outside of MPAs, the intrinsic natural variability of seascapes and inside the seascape of the habitats which compose the seascape, should be preserved; this implies reducing the human stressors which usually lead to a homogenization of the environment. Indeed protection of habitat through MPAs may be not enough and management requires as well reducing indirect habitat transformations (e.g. impacts of pollutions, invasive species, etc.).

This PhD thesis and future works gathering knowledge on juvenile habitats identification, and on factors affecting nursery value of habitats, will provide managers essential data to establish a multi-taxa seascape approach for the optimized design of management measures in order to protect biodiversity and associated ecosystem services.

VI.3. PERSPECTIVES

The aim of this thesis was to understand in Minorca island the influence of potentially important factors determining the density distributions and dynamics of labrids and sparids juveniles among their juveniles habitats: seagrass meadows, arborescent macroalgae forests and mixed bottoms of sand, pebbles and boulders. These factors were: 1) the three-dimensional structure of the environment *sensu lato*, from the large scale coast configuration and depth to the lower scale habitat structure; 2) biological interactions in terms of presence of predators and adult con-specifics; and finally 3) physical constrains in terms of meteorological conditions.

To go further beyond the conclusions of this work, various challenging questions remain opened. First, even before studying the influence of factors on juveniles in their nursery habitats, a basic step is often missing for many habitats and fish species in the coastal Mediterranean: for many species, we still don't know their main juvenile habitats (e.g. the emblematic *Sciaena umbra*). Indeed, juvenile studies in the Mediterranean, in general, are scarce and focused in its Western part (Bussotti and Guidetti, 2010; Cheminée, 2012; Felix-Hackradt, 2013; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Macpherson and Raventos, 2005; Thiriet, 2014). Secondly, for many fish species, studies comparing juvenile densities are usually limited to a handful of habitat and fail to truly compare all the potential juvenile habitats available in a given site among the entire seascape mosaic. Consequently, more habitats comparisons are needed to state the importance of each habitat for each species, e.g. *Cymodocea nodosa* vs. *Posidonia oceanica* meadows, *Cystoseira* spp. forests vs. *P. oceanica* meadows, the different phytological Phaeophyceae assemblages in rocky bottoms (e.g. Sphacelariales, vs. Dictyotales, different species of *Cystoseira*), etc. Finally, other habitats have been poorly studied; e.g, the chlorophyta communities, such as *Cladophora* formations or *Caulerpa* spp. meadows. Consequently, as a general rule, more studies at different Mediterranean sites (western and eastern ones) and accomplishing more habitat comparisons are needed.

This matches with another point of current interest: global changes are affecting the Mediterranean habitats and fish assemblages. For example, eastern sites are under the increasing pressure of invasive fish species (adult and juvenile stages) (e.g. *Siganus* spp., *Fistularia* sp.). These species may alter native juvenile assemblage through both direct

competition (juveniles) and predation (adults) and through indirect habitat transformation (e.g. over-grazing) (Sala et al., 2011). Besides, the spread of invasive species is facilitated by an increasing sea-surface temperature in the Mediterranean (Bodilis et al., 2011). There is consequently a gradient of influences from both invasive species (from east to west) and temperatures (oriented north-ward). This requires comparative studies among various habitats in invaded *versus* uninvaded sites, along this latitudinal gradient.

Furthermore, many of the available studies about essential habitats for juveniles analyze only fish densities, i.e. only one of the four juvenile parameters (initial density, growth, mortality, connectivity) contributing to the real nursery value of a given habitats (Beck et al., 2001). Indeed, measuring juvenile density is only a proxy of settlers supply or in the best case a proxy of settlers supply combined with some mortality. The others components of the nursery value, i.e., growth, survival and movement to adult habitats should be also investigated (Beck et al., 2001). This is the key to truly assess the recruitment potential of coastal areas. Growth could be studied through otolimetry and biomass measures (Vigliola, 1998), survival by means of temporal monitoring (Macpherson et al., 1997) or manipulative experimentations (Thiriet, 2014); movement to adult habitats could be studied through visibly deployed fluorescent elastomers (VIFE) (Calò et al., 2013). This last technique recently implemented for juvenile fish, combined with detailed cartography of habitats in the seascape, may also allow us to study the juvenile movement and spatially explicit usage of habitat patches and corridors (Nagelkerken et al., 2015) to better understand the usage of seascape by juveniles. In this thesis we mainly studied the influence of factors on the density patterns of juveniles, although we accomplished some efforts to better understand the influence of the studied factors on the other components of the nursery value (growth, survival, some ontogenic habitat shifts in Chapters III, IV and V), or on juvenile behavior (Chapter III). Consequently, the techniques mentioned above may also be essential to completely understand the influence of the studied factors on the final production of juveniles in the studied habitats.

In this thesis we highlighted the importance of three-dimensional structure of the environment *sensu lato* at large scales (coast configuration, depth) and local scales inside a given habitat (habitat structure) in determining juvenile density distributions. Much of the density variations within differently structured patches or sites of a given habitat may be explained by the quality of habitats (the trade-off between shelter and food availability)

(Dahlgren and Eggleston, 2000). We argue that the effect of habitat structure we observed may be related to both food and shelter availability, although we were not able to distinguish the effect of both of them. Improving knowledge on diet of fish and food availability will help us to confirm such hypothesis. In the same sense, coupling studies of behaviors and functional morphology of fish may help us to improve knowledge about the morphological adaptations allowing successful foraging or sheltering (camouflage, mobility) in different habitats or patches within habitats.

Besides, the influence of coast configuration was only tested for one species: *D. sargus*. The influence of coast configuration should be studied for more species. Indeed, in Chapter II we hypothesised that emplacement of sites in enclosed bay (near *vs* far from the opening toward the sea) influenced juveniles of *C. nodosa* meadows. It should be further investigated in order to test the hypothesis that areas near the open sea receive more settlers. Monitoring of plankton (catch nets) (Calò et al., 2013; López-Sanz et al., 2009) could be done in the different regions of such embayment during settlement events, or alternatively, ones may use temporal monitoring by means of UVC.

Finally, it could be interesting to know at which point the intrinsic variability of juvenile density distributions among the seascape, or inside a given habitats is later on translated or not as variability in the density of adult population (e.g. homogeneous habitats, *versus* patchy habitats) or if adult mobility or post-settlement processes such as denso-dependent processes can reshape these patterns.

As a regards to the other factors studied in this thesis, we failed in our aim to study how biological interactions in terms of presence of adult predators and con-specifics competitors may influence juveniles; indeed, studied predator were very scarce at considered depths and their putative spatial partitioning (in *vs* outside reserve) was not evident. It would consequently be advisable to accomplish studies in and out MPA were predators of juveniles are present at the same depths, in order to state the influence of predators. Laboratory experiments such as those accomplished by Thiriet (2014) for predators, may as well help to understand the competitiveness between adults and juveniles. Such studies should be tested also on the other components of the nursery value, such as growth and survival. Indeed, for example, some competitive effects of adults con-specifics has been reported on growth patterns (Jones, 1987).

Finally, the physical factors in terms of meteorological influences showed the importance of hydrodynamics determined by winds, causing alternatively mortality or picking out larvae from coasts. To better understand such alternative responses to meteorological conditions, catches of plankton near the coast immediately previous and after rough hydrodynamic events, coupled with daily temporal monitoring of settlers will clarify and further test such hypothesis. Furthermore, otoliths microchemistry may help us to localize larvae origin, to better understand the differential influence of such hydrological conditions. Finally, VIFE techniques may allow us to understand the behavior of fish of different sizes under the influence of rough hydrodynamic events: do juveniles hide in deeper areas when sea is agitated? At what sizes they may occur?

As a regards to physical meteorological factors, we failed to determinate if temperatures had an effect, since study sites displayed almost the same temperatures. Furthermore, we installed the temperature sensors in slightly deeper areas than nursery habitats for *D. sargus*. Surface waters have a more variable temperatures (personal observation). The installation of temperature sensors closer to the nursery juveniles habitats, at 1 meter depth, or alternatively, comparisons between contrasted areas with different temperatures, or more temporal series may help us to better understand how may the variation of surface waters temperatures affect the nursery value.

Finally, Mediterranean management's efforts must be centred in improving the knowledge of factors influencing nursery value and in improving the knowledge of the nursery role of different habitats. Furthermore it is necessary the implementation of direct measures which avoid the physical destruction of juveniles habitats. In order to assure the sustainability of biodiversity various juvenile habitats must be protected. Furthermore regional habitat availability must be taken into account and habitats with a lower production of juveniles must not be completely excluded of the management's plans. Finally it is essential to define the uses that are considered moderate and which could be beneficial ecologically and economically, to provide a sustainable use of resources without depleting marine resources.

Chapter VII. General Conclusions

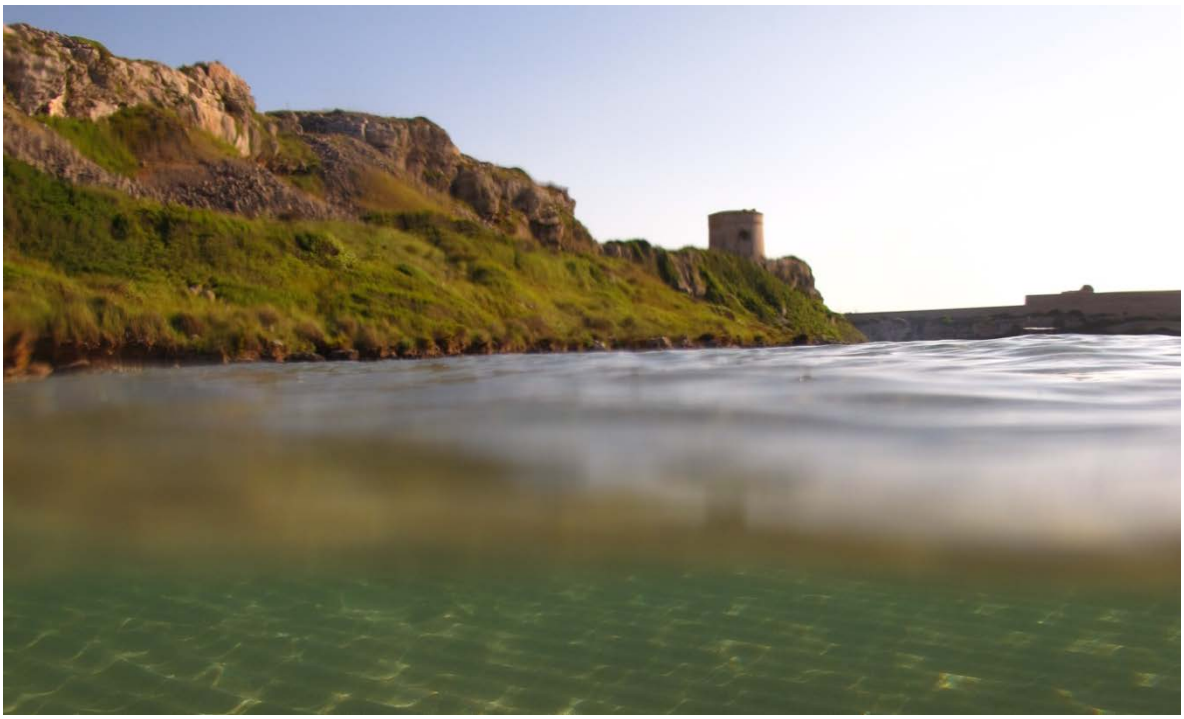

Photo VII-1. Cala Taulera, Minorca island. April 2013. Photo: Adrien Cheminée.

Chapter VII. General Conclusions

The main results of this thesis are as follows:

1) Habitat type was a major determinant of the composition of the juvenile fish assemblages.
2) Among the three studied habitats various seascape attributes operated at different spatial scales shaping juvenile density distributions.
3) The juvenile fish assemblages of shallow (0-1 m) *Cymodocea nodosa* meadows responded to habitat structure at seascape scale, but not at microhabitat scale.
4) The presence of boulders within these shallow seagrass meadows increased the total density and richness of juvenile fish.
5) The juveniles of *Symphodus* species were more abundant when boulders were present in the seagrass meadows, whereas the abundance of *Diplodus annularis* juveniles was not affected by the presence or absence of boulders.
6) Depth and canopy structure were the major determinants of juvenile densities in infralittoral (0-15 m depth) *Cystoseira* forests.
7) Juveniles of *Symphodus* individuals preferred dense stands of *Cystoseira* forests whereas juveniles of *Coris julis* and *Thalassoma pavo* preferred sparser ones.
8) Juvenile *Symphodus* species of any size and smallest juveniles of *T. pavo* displayed cryptic behavior in *Cystoseira* forests.
9) Juveniles of *T. pavo* displayed a more cryptic behavior in dense forests, whereas in the less complex forests they switched towards wandering or transitory behaviors.
10) Wind-induced hydrodynamics, configuration of the coastline (i.e., orientation, exposure), habitat structure, depth and density dependent mortality after settlement shaped the density of *D. sargus* juveniles in shallow mixed habitats of rocks, pebbles and sand.
11) SE winds (of 10 $m.s^{-1}$) shaping 1.5 m waves (10 s period), lowered *D. sargus* juvenile densities. More particularly, northeast orientation of the coastline associated with these SE winds, resulted in off-shore winds which were unfavorable for the larval supply.
12) Sheltered coves supported lower densities of *D. sargus* settlers than exposed coves and consequently displayed a lower recruitment level.

13) Smaller sizes of *D. sargus* juveniles preferred the most heterogeneous substratum among its nursery habitat.
14) Post-settlement density-dependent mortality highly shaped the recruitment level of *D. sargus* juveniles.
15) There is not a single habitat that serves as nursery to all the species of littoral fishes considered here. Thus, habitat heterogeneity at a scale of tens of kilometres is necessary to ensure the recruitment of a diversified fish fauna.
16) In order to protect juvenile fish in a given locality, seascape attributes at different scales must be taken into account in management planning. They include: coast configuration and bathymetry, seascape habitat composition, habitat relative availability, local nursery value of each habitat for each species and intrinsic habitat structure variability.
17) Management actions to protect juvenile fish must focus not only on the banning of the physical destruction of juvenile habitats, but as well on avoiding the transformation of their tri-dimensional structure.

Chapter VIII. Supplementary data

Photo VIII-1.Es Talaier, Minorca island. April 2013. Photo: Adrien Cheminée.

Chapter VIII. Supplementary data

VIII.1. Supplementary tables and figures for Chapter III

Table VIII-1. PERMANOVA table of results: influence of location (2012), protection (2013) and depth on univariate habitat structure descriptors: forest height, cover and PC1- main tests.
Factor location (lo): 2 levels (location B and location C); Factor protection (pr): 2 levels (inside MPA, outside MPA); Factor depth (de): 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m); Factor site (si) with 6 levels (3 sites by level of the factor location or protection). *P*-values were obtained by 999 permutations of residuals under a reduced model. Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Response variable considered	Year	Source of var.	df	MS	Pseudo-F	P (perm)
Forest height	2012	Location (lo)	1	450.82	32.28	0.009**
		Depth (de)	2	237.46	8.61	0.01*
		Site si(lo)	4	13.97	7.12	0.001***
		loxde	2	33.78	1.23	0.343
		Si(lo)xde	8	27.57	14.06	0.001***
		Residuals	126	1.96		
		Total	143			
	2013	Protection (pr)	1	408.22	16.61	0.018*
		Depth (de)	2	156.46	6.39	0.015*
		Site si(pr)	4	24.58	20.48	0.001***
		prxde	2	18.57	0.76	0.511
		Si(pr)xde	8	24.49	20.40	0.001***
		Residuals	126	1.20		
		Total	143			
Forest cover	2012	Location (lo)	1	383.51	1.02	0.35
		Depth (de)	2	1568.9	6.16	0.025*
		Site si(lo)	4	375.69	5.60	0.002**
		loxde	2	79.34	0.31	0.735
		Si(lo)xde	8	254.6	3.80	0.002**
		Residuals	126	67.04		
		Total	143			
	2013	Protection (pr)	1	262.56	0.62	0.468
		Depth (de)	2	1635.8	2.94	0.117
		Site si(pr)	4	420.3	6.52	0.001***
		prxde	2	95.68	0.17	0.84
		Si(pr)xde	8	556.86	8.63	0.001***
		Residuals	126	64.49		
		Total	143			

Table VIII-1. (Continued)						
PC1	2012	Location (lo)	1	35.2	10.90	0.035*
		Depth (de)	2	34.47	7.45	0.019*
		Site si(lo)	4	3.23	7.15	0.001***
		loxde	2	1.57	0.34	0.739
		Si(lo)xde	8	4.63	10.24	0.001***
		Residuals	126	0.45		
		Total	143			
	2013	Protection (pr)	1	35.35	9.34	0.032*
		Depth (de)	2	21.55	3.53	0.084·
		Site si(pr)	4	3.79	9.83	0.001***
		prxde	2	0.58	$9.44 \cdot 10^{-2}$	0.915
		Si(pr)xde	8	6.11	15.86	0.001***
		Residuals	126	0.39		
		Total	143			

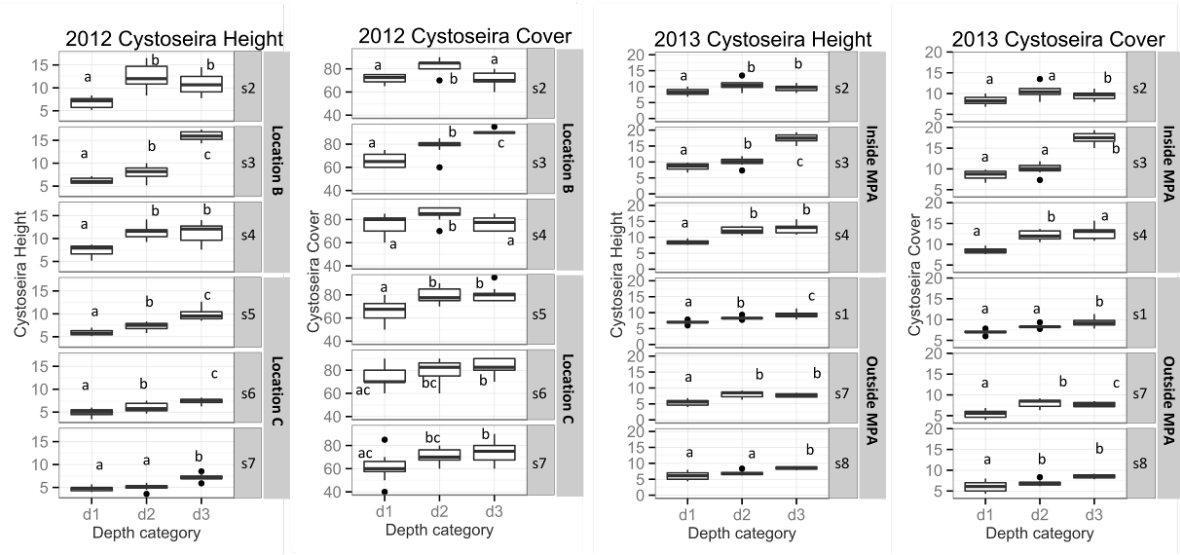

Fig. VIII-1. Boxplots of *Cystoseira* forest height, and cover within samples according to locations (2012)/ protection (2013), depth categories (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m) and sites. Box plots indicate the median (bold line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the inter quartile range (whiskers), and remaining outliers (open circles). Pair-wise tests between treatments are given in box plots (different lower case characters indicate significant differences between treatments).

Table VIII-2. PERMANOVA table of results: influence of habitat structure, location (2012), protection (2013) and depth on univariate juvenile assemblage descriptors: total density and richness- main tests.

Factor location (lo): 2 levels (location B and location C); Factor protection (pr): 2 levels (inside MPA, outside MPA); Factor depth (de): 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m); Factor site (si) with 6 levels (3 sites by level of the factor location or protection). *P*-values were obtained by 999 permutations of residuals under a reduced model. Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Considered Response variables	Year	Source of var.	df	MS	Pseudo-F	P (perm)
Total density	2012	PC1(covariate)	1	$6.15 .10^{-2}$	$6.87.10^{-3}$	0.924
		Location (lo)	1	22.65	1.87	0.317
		Depth (de)	2	11.54	1.14	0.327
		Site si(lo)	4	12.74	1.63	0.186
		loxde	2	7.46	0.74	0.486
		Si(lo)xde	8	10.12	1.30	0.255
		Residuals	125	7.81		
		Total	143			
	2013	PC1(covariate)	1	317.93	2.27	0.143
		Protection (pr)	1	11.54	$4.47.10^{-2}$	0.765
		Depth (de)	2	454.32	3.21	0.107
		Site si(pr)	4	284.79	3.31	0.013*
		prxde	2	15.74	0.15	0.858
		Si(pr)xde	8	136.02	1.58	0.134
		Residuals	125	86.17		
		Total	143			
Richness	2012	PC1(covariate)	1	1.26	1.48	0.233
		Location (lo)	1	3.48	2.96	0.192
		Depth (de)	2	0.91	0.54	0.621
		Site si(lo)	4	1.24	1.69	0.144
		loxde	2	0.72	0.42	0.684
		Si(lo)xde	8	1.71	2.33	0.019*
		Residuals	125	0.73		
		Total	143			
	2013	PC1(covariate)	1	0.26	0.11	0.754
		Protection (pr)	1	0.16	$3.04.10^{-2}$	0.995
		Depth (de)	2	4.37	2.23	0.161
		Site si(pr)	4	6.02	5.27	0.001***
		prxde	2	3.05	1.59	0.294
		Si(pr)xde	8	1.85	1.62	0.113
		Residuals	125	1.14		
		Total	143			

Table VIII-3. PERMANOVA table of results: effect of habitat structure, location (2012), protection (2013) and depth on juvenile densities per taxa.
Factor location (lo): 2 levels (location B and location C); Factor protection (pr): 2 levels (inside MPA, outside MPA); Factor depth (de): 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m); Factor site (si) with 6 levels (3 sites by level of the factor location or protection). *P*-values were obtained by 999 permutations of residuals under a reduced model. Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Considered Response variable	Year	Source of var.	df	MS	Pseudo-F	P (perm)
Coris julis densities	2012	PC1(covariate)	1	56.92	14.15	0.001***
		Location (lo)	1	8.89	1.05	0.497
		Depth (de)	2	51.62	7.93	0.008**
		Site si(lo)	4	9.31	3.83	0.005**
		loxde	2	6.76	1.00	0.394
		Si(lo)xde	8	6.57	2.71	0.008**
		Residuals	125	2.43		
		Total	143			
	2013	PC1(covariate)	1	7.07	1.27	0.258
		Protection (pr)	1	9.10	0.80	0.371
		Depth (de)	2	37.10	5.66	0.024*
		Site si(pr)	4	12.76	4.44	0.003**
		prxde	2	13.90	2.10	0.204
		Si(pr)xde	8	6.29	2.19	0.039*
		Residuals	125	2.88		
		Total	143			
Thalassoma pavo densities	2012	PC1(covariate)	1	73.45	33.00	0.001***
		Location (lo)	1	0.57	0.26	0.628
		Depth (de)	2	22.17	5.58	0.021*
		Site si(lo)	4	2.25	1.01	0.39
		loxde	2	4.95	1.19	0.347
		Si(lo)xde	8	4.07	1.83	0.077·
		Residuals	125	2.22		
		Total	143			
	2013	PC1(covariate)	1	55.01	3.68	0.069·
		Protection (pr)	1	1.96	$4.96.10^{-2}$	0.82
		Depth (de)	2	121.54	12.77	0.002**
		Site si(pr)	4	45.25	12.44	0.001***
		prxde	2	17.72	1.95	0.222
		Si(pr)xde	8	8.63	2.37	0.02*
		Residuals	125	3.64		
		Total	143			
Symphodus spp. densities	2013	PC1(covariate)	1	434.93	33.87	0.001***
		Location (lo)	1	0.91	0.11	0.692
		Depth (de)	2	56.30	6.90	0.018*
		Site si(lo)	4	6.97	0.46	0.785
		loxde	2	29.36	3.55	0.09·
		Si(lo)xde	8	8.04	0.53	0.846
		Residuals	125	15.04		
		Total	143			

Table VIII-4. PERMANOVA table of results: influence of habitat structure, location (2012), protection (2013) and depth on juvenile total length per taxa.
Factor location (lo): 2 levels (location B and location C); Factor protection (pr): 2 levels (inside MPA, outside MPA); Factor depth (de): 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m); Factor site (si) with 6 levels (3 sites by level of the factor location or protection). *P*-values were obtained by 999 permutations of residuals under a reduced model. Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Considered Response variable	Year	Source of var.	Df	MS	Pseudo-F	P (perm)
Coris julis TL	2012	No test				
	2013	PC1(covariate)	1	289.06	2.64	0.115
		Protection (pr)	1	1.01	$7.54.10^{-3}$	1
		Depth (de)	2	631.55	3.86	0.024*
		Site si(pr)	4	140.82	1.67	0.155
		prxde	2	1026.8	7.18	0.023*
		Si(pr)xde	7	113.01	1.34	0.195
		Residuals	253	84.19		
		Total	270			
Thalassoma pavo TL	2012	PC1(covariate)	1	1689.3	3.92	0.066·
		Location (lo)	1	2647.1	2.77	0.158
		Depth (de)	2	1268.7	6.41	0.014*
		Site si(lo)	4	1020.1	8.77	0.001***
		loxde	2	163.6	1.23	0.358
		Si(lo)xde	8	125.54	1.08	0.376
		Residuals	249	116.27		
		Total	267			
	2013	PC1(covariate)	1	4563.4	16.18	0.001***
		Protection (pr)	1	2203.9	1.74	0.258
		Depth (de)	2	72.88	0.44	0.648
		Site si(pr)	4	1122.4	20.02	0.001***
		prxde	2	519.62	4.40	0.062·
		Si(pr)xde	8	93.80	1.67	0.135
		Residuals	424	56.06		
		Total	442			
Symphodus spp. TL	2013	No test				

Table VIII-5. PERMANOVA table of results: influence of habitat structure, fish Total Lenght (TL), location (2012), protection (2013) and depth on juvenile multivariate behavior composition per taxa.
Factor location (lo): 2 levels (location B and location C); Factor protection (pr): 2 levels (inside MPA, outside MPA); Factor depth (de): 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m); Factor site (si) with 6 levels (3 sites by level of the factor location or protection). *P*-values were obtained by 999 permutations of residuals under a reduced model. Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Considered Response variables	Year	Source of var.	Df	MS	Pseudo-F	P (perm)
Coris julis behavior composition	2012	No test				
	2013	PC1 (covariate)	1	6469.7	1.85	0.169
		TL (covariate)	1	$1.08 \cdot 10^5$	39.72	0.001***
		Protection (pr)	1	5196.2	1.20	0.327
		Depth (de)	2	7847	1.86	0.127
		Site si(pr)	4	4540.8	1.71	0.102
		prxde	2	2824.7	0.86	0.538
		Si(pr)xde	7	3249.6	1.22	0.252
		Residuals	218	2654.4		
		Total	236			
Thalassoma pavo behavior composition	2012	PC1(covariate)	1	25904	5.27	0.01*
		tl(covariate)	1	$1.15 \cdot 10^5$	29.52	0.001***
		Location (lo)	1	302.55	$3.61.10^{-2}$	0.97
		Depth (de)	2	14405	3.26	0.014*
		Site si(lo)	4	9068.3	3.47	0.001***
		loxde	2	2267	0.59	0.703
		Si(lo)xde	8	3946.1	1.51	0.069·
		Residuals	248	2615.2		
		Total	267			
	2013	PC1(covariate)	1	27046	14.55	0.001**
		tl(covariate)	1	79556	46.76	0.001***
		Protection (pr)	1	895.05	0.18	0.911
		Depth (de)	2	665.6	0.20	0.862
		Site si(pr)	4	5033.3	5.16	0.002**
		prxde	2	7840.2	1.71	0.148
		Si(pr)xde	8	3738.2	3.83	0.001***
		Residuals	423	975.27		
		Total	442			
Symphodus spp.	2012	No test				
	2013	PC1(covariate)	1	22617	0.56	0.61
		tl(covariate)	1	12404	2.24	0.128
		Protection (pr)	1	1496.5	$4.10 \cdot 10^{-2}$	0.943
		Depth (de)	2	18290	0.53	0.579
		Site si(pr)	4	28729	18.25	0.001***
		prxde	2	16287	1.24	0.383
		Si(pr)xde	7	10525	4.96	0.001***
		Residuals	250	2122.3		
		Total	268			

Table VIII-6. PERMANOVA table of results: influence of protection and depth on multivariate adult biomass assemblage and univariate densities, and TL of predators and con-specifics.
Factor location (lo): 2 levels (location B and location C); Factor protection (pr): 2 levels (inside MPA, outside MPA); Factor depth (de): 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m); Factor site (si) with 6 levels (3 sites by level of the factor location or protection). *P*-values were obtained by 999 permutations of residuals under a reduced model. Significance: ·$P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Considered Response variables	Year	Source of var.	df	MS	Pseudo-F	P (perm)
Multivariate biomass Assemblage	2013					
		Protection (pr)	1	8.89	1.52	0.285
		Depth (de)	2	6.45	2.47	0.038*
		Site si(pr)	4	5.83	2.84	0.005**
		prxde	2	2.38	0.91	0.486
		Si(pr)xde	8	2.61	1.28	0.262
		Residuals	36	2.05		
		Total	53			
Serranus spp. density	2013	Protection (pr)	1	$2.30 \cdot 10^{-18}$	$3.58 \cdot 10^{-15}$	1
		Depth (de)	2	$3.76 \cdot 10^{-4}$	1.07	0.377
		Site si(pr)	4	$6.43 \cdot 10^{-4}$	3.05	0.019*
		prxde	2	$4.63 \cdot 10^{-5}$	0.13	0.878
		Si(pr)xde	8	$4.50 \cdot 10^{-4}$	1.66	0.149
		Residuals	36	$2.11 \cdot 10^{-4}$		
		Total	53			
Serranus spp. TL	2013	Protection (pr)	1	83.70	0.30	0.589
		Depth (de)	2	653.95	0.76	0.511
		Site si(pr)	4	260.41	0.67	0.584
		prxde	2	805.61	0.93	0.441
		Si(pr)xde	7	910.46	2.36	0.062·
		Residuals	41	385.8		
		Total	57			
C. julis density	2013	Protection (pr)	1	$6.22 \cdot 10^{-4}$	$8.29 \cdot 10^{-2}$	0.789
		Depth (de)	2	$4.13 \cdot 10^{-2}$	6.45	0.023*
		Site si(pr)	4	$7.51 \cdot 10^{-3}$	2.55	0.067·
		prxde	2	$2.72 \cdot 10^{-3}$	0.43	0.641
		Si(pr)xde	8	$6.40 \cdot 10^{-3}$	2.18	0.055·
		Residuals	36	$2.94 \cdot 10^{-3}$		
		Total	53			
C. julis TL	2013	Protection (pr)	1	1724.5	0.70	0.437
		Depth (de)	2	398.3	0.38	0.69
		Site si(pr)	4	2492.4	6.88	0.001***
		prxde	2	1588.7	1.51	0.293
		Si(pr)xde	8	1082.2	2.99	0.004**
		Residuals	413	362.34		
		Total	430			

Table VIII-6. (Continued)						
Symphodus spp. density	2013	Protection (pr)	1	$3.21 \cdot 10^{-3}$	1.29	0.283
		Depth (de)	2	$1.30 \cdot 10^{-3}$	1.35	0.304
		Site si(pr)	4	$2.49 \cdot 10^{-3}$	3.85	0.021*
		prxde	2	$1.44 \cdot 10^{-4}$	0.15	0.867
		Si(pr)xde	8	$9.59 \cdot 10^{-4}$	1.48	0.174
		Residuals	36	$6.48 \cdot 10^{-4}$		
		Total	53			
Symphodus spp. TL	2013	Protection (pr)	1	51.91	$4.73 \cdot 10^{-2}$	0.786
		Depth (de)	2	4398.4	3.47	0.138
		Site si(pr)	4	863.73	0.51	0.748
		prxde	2	945.15	0.75	0.511
		Si(pr)xde	5	1111.5	0.65	0.675
		Residuals	66	1698.3		
		Total	80			
T. pavo density	2013	Protection (pr)	1	$1.09 \cdot 10^{-2}$	1	0.345
		Depth (de)	2	$5.03 \cdot 10^{-2}$	16.54	0.002
		Site si(pr)	4	$1.09 \cdot 10^{-2}$	4.93	0.004
		prxde	2	$7.51 \cdot 10^{-3}$	2.47	0.157
		Si(pr)xde	8	$3.04 \cdot 10^{-3}$	1.37	0.224
		Residuals	36	$2.22 \cdot 10^{-3}$		
		Total	53			
T. pavo TL	2013	Protection (pr)	1	1386.5	4.11	0.057·
		Depth (de)	2	766.39	2.65	0.147
		Site si(pr)	4	304.59	0.83	0.477
		prxde	2	129.13	0.45	0.636
		Si(pr)xde	7	250.96	0.69	0.668
		Residuals	235	364.81		
		Total	251			

Table VIII-7. Mean adult densities (ind. m^{-2}) and biomass (g. m^{-2}) for each level of the factors protection and depth.
Depth: 3 levels (d1: 3-5 m, d2: 6-8 m, d3: 10-12 m); Species: cj= *Coris julis*; bg= *Blenniidae-Gobiidae-Tripterygiidae* spp.; da= *Diplodus annularis*; dp= *Diplodus puntazo*; ds= *Diplodus sargus*; dv= *Diplodus vulgaris*; lb= *Labrus* spp.; sa= *Sarpa salpa*; se= *Serranus* spp.; ss= *Symhodus* spp.; tp=*Thalassoma pavo.*

		Inside MPA						Outside MPA					
	sps	d1		d2		d3		d1		d2		d3	
		mean	se	mean	se	mean	se	mean	Se	mean	se	mean	se
Density	cj	0.070	0.015	0.187	0.027	0.131	0.017	0.106	0.014	0.180	0.030	0.12	0.01
	da	0	0	0	0	0	0	0	0	0	0	0.002	0.002
	dp	0	0	0	0	0	0	0	0	0	0	0.002	0.002
	ds	0.006	0.003	0	0	0.002	0.002	0.024	0.017	0.009	0.006	0.007	0.004
	dv	0.019	0.015	0.017	0.009	0.009	0.006	0.019	0.007	0.015	0.003	0.015	0.009
	lb	0.002	0.002	0.002	0.002	0	0	0.002	0.002	0	0	0	0
	mu	0	0	0	0	0.004	0.004	0	0	0	0	0	0
	sa	0.076	0.039	0.024	0.022	0.011	0.006	0.011	0.011	0.074	0.074	0	0
	se	0.017	0.006	0.015	0.004	0.022	0.005	0.013	0.005	0.017	0.006	0.024	0.007
	ss	0.011	0.007	0.022	0.010	0.019	0.008	0.020	0.008	0.043	0.011	0.035	0.013
	tp	0.141	0.030	0.043	0.008	0.007	0.004	0.124	0.015	0.106	0.028	0.046	0.008
Biomass	cj	0.938	0.258	1.797	0.230	1.368	0.339	1.211	0.152	2.206	0.338	1.611	0.178
	da	0	0	0	0	0	0	0	0	0	0	0.501	-
	dp	0	0	0	0	0	0	0	0	0	0	1.074	-
	ds	0.703	0.134	0	0	0.347	-	2.824	1.273	1.039	0.639	0.923	0.337
	dv	4.470	3.436	2.967	2.381	3.163	2.036	1.601	0.481	0.844	0.218	1.656	0.668
	lb	0.525	NA	1.645	-	0	0	1.645	-	0	0	0	0
	mu	0	0	0	0	2.307	-	0	0	0	0	0	0
	sa	20.661	10.205	9.846	4.600	4.541	1.311	2.651	-	17.674	-	0	0
	se	1.538	0.310	0.569	0.099	0.755	0.169	0.675	0.166	0.834	0.202	1.323	0.343
	ss	1.800	0.937	0.890	0.240	1.346	1.008	1.951	0.733	1.464	0.328	2.386	0.854
	tp	1.640	0.565	0.420	0.089	0.156	0.036	1.671	0.323	1.574	0.496	0.575	0.173

VIII.2. Supplementary figures for Chapter V

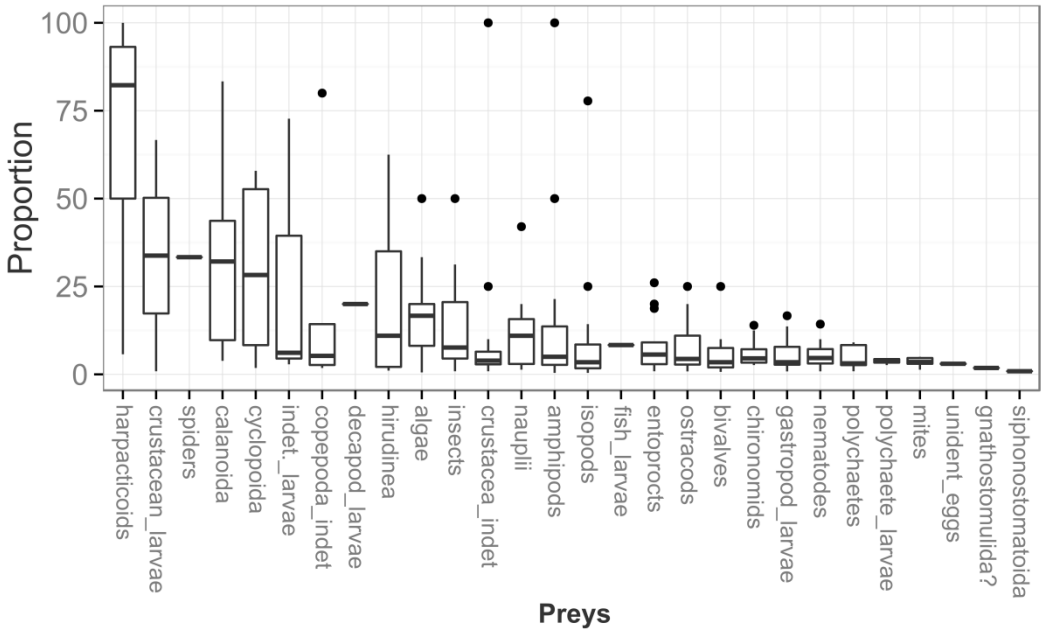

Fig. VIII-2. Boxplot of the different proportion of preys in the stomach content of *Diplodus sargus* juveniles (10-30 mm TL).

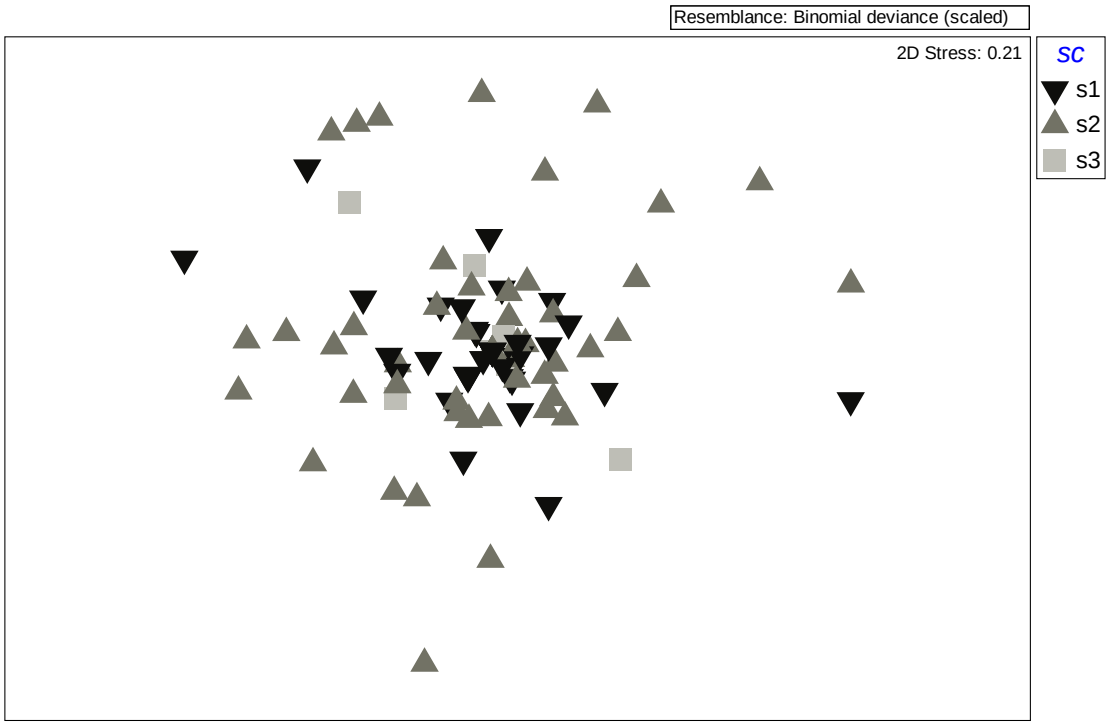

Fig. VIII-3. nMDS ordination plot of stomach content prey assemblage for *Diplodus sargus* juveniles (10-30 mm). Different tones of gray and symbols represent different size class (sc) of fishes: s1: 10-16 mm TL; s2: 17-23 mm TL; s3: 24-30 mm TL.

Chapter IX. References

Photo IX-1. Addaia, Minorca island. April 2013. Photo: Adrien Cheminée.

Chapter IX. References

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